1990

Juvenile Penaeid Shrimp Ecology in a Louisiana Coastal Marsh Management Area.

Everett Eric Knudsen
Louisiana State University and Agricultural & Mechanical College

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313 761-4700 800 521-0600

Order Number 9123210

Juvenile penaeid shrimp ecology in a Louisiana coastal marsh management area

Knudsen, Everett Eric, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1990

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

JUVENILE PENAEID SHRIMP ECOLOGY

IN A LOUISIANA COASTAL MARSH MANAGEMENT AREA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

Wildlife and Fisheries Science

by
Everett Eric Knudsen
B.S., University of Massachusetts, 1974
M.S., Louisiana State University, 1976
December 1990

Acknowledgments

Much of this work was supported by the U. S. Soil Conservation Service. I thank the numerous employees of the Louisiana State University Cameron-Creole fisheries field laboratory for their hard work under difficult circumstances to process the large samples needed to do this work and to collect, mark, and recapture shrimp; employees of Sabine National Wildlife Refuge for their support; and Miami Corporation for access across their land to the study site.

I sincerely appreciate all the encouragement, support, and guidance provided by Dr. William H. Herke, my major professor and mentor. The other members of my committee, Drs. C. Fred Bryan, Richard E. Condrey, Robert B. Hamilton, Mark K. Johnson, and William E. Kelso made significant contributions to my graduate program and in reviewing manuscripts and this dissertation. I extend special appreciation to my friend and associate, Mr. Barton Rogers, for his cooperation and assistance throughout this project. Thanks also go to Michelle LaGory for her artwork and Dawn Brady and Rudy Moralez for typing some of the drafts. I appreciate the support of my current employer, the U.S. Fish and Wildlife Service, for providing facilities for completion of this dissertation.

ABSTRACT

Juvenile penaeid shrimp were studied by a variety of methods in a southwest Louisiana, brackish marsh. Most of the work was conducted in two study ponds, one with a fixed-crest weir and the other without. In mark and recapture studies, both brown shrimp *Penaeus aztecus* and white shrimp *P. setiferus* were found to grow faster in marsh behind a fixed-crest weir. There was no apparent weir effect on mortality of either species. Brown shrimp emigrated an average of 12 d later from marsh behind the weir; white shrimp were sometimes delayed by the weir. The peak of brown shrimp emigration from both weired and unweired marsh peaked coincided with both new and full moons. I used four methods of estimating juvenile shrimp standing stocks and found that shrimp were usually less abundant in the weired than the unweired pond. The reduction in observed emigration of shrimp from a weired area was likely caused by restricted immigration past the weir. I used density estimates from the unweired study pond and a nearby marsh pond to confirm that export estimates in previous studies of the unweired pond were reasonable, although conservative, estimates of normal numbers of shrimp emigrating from similar marsh ponds. Graphic analysis, linear statistics, and superposed epoch analysis were used to study effects of environmental variables on white shrimp emigration. White shrimp emgration from the marsh was associated with decreasing temperatures, high water outflow, decreasing and/or low barometric pressure, and rainfall.

TABLE OF CONTENTS

Acknowledgments ii

Abstract iii

CHAPTER I. Introduction 1

CHAPTER II. Study site and General Methods. 3

CHAPTER III. Effects of a fixed-crest weir on juvenile brown shrimp growth, mortality, and emigration. 8

Introduction. 8

Methods 9

Growth 10

Relative mortality 12

Relative emigration patterns 13

Results 14

Growth 14

Relative mortality 16

Relative emigration patterns 19

Length at emigration 20

Discussion. 22

Conclusions 28

Chapter IV. Effects of a fixed-crest weir on juvenile white shrimp mortality, growth, and emigration. 30

Introduction. 30

Methods 31

Mortality. 33

Growth 33

Emigration 36

Results 36

Mortality. 36
Growth 37
Emigration 44
Discussion. 52
Conclusions 56
Chapter V. Abundance and distribution of juvenile penaeid shrimp in weired, unweired, and natural Louisiana marsh waters . 58
Introduction. 58
Methods 60
Results 64
Density differences between weired and unweired ponds. . 64
Trawl sampling. 64
Beam trawl sampling 72
Drop cylinder sampling. 72
Abundance of shrimp in natural marsh 79
Trawl sampling. 79
Drop cylinder sampling. 83
Discussion. 87
Conclusions 91
Chapter VI. Relation between juvenile white shrimp emigration and environmental variables in a coastal Louisiana marsh pond 92
Introduction. 92
Methods 94
Environmental effects on numbers emigrating. 94
Graphic analysis. 95
Correlations. 95
Stepwise multiple regression. 96

Superposed epoch analysis. 96
Length at emigration 99
Results 100
Environmental effects on numbers emigrating. 100
Salinity 106
Temperature. 110
Volume of inflow and outflow 118
Barometric pressure. 120
Precipitation 123
pH 123
Dissolved oxygen 126
Length at emigration 128
Discussion. 134
Conclusions 139
References. 141
Vita. 151

CHAPTER I. Introduction

Numerous studies have been conducted on the life-history of commercially important brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) along the U.S. Atlantic and Gulf of Mexico coasts. Yet little work has focused on the ecology of juvenile penaeid shrimp in their interior marsh nursery habitat. In Louisiana, where approximately 40% of the U.S. commercial penaeid shrimp harvest is landed, nursery habitat is characterized by vast areas of intertidal marsh vegetation interspersed with numerous tidal creeks, canals, and shallow-water lakes and ponds. This primary nursery habitat is being threatened by 1) increasing erosion of coastal marshes into large areas of open, shallow water with reduced edge habitat, and 2) reduced access to nursery habitat caused by water control structures intended to reduce saltwater intrusion via tidal bayous and canals. The fisheries effects of Louisiana coastal erosion, and some currently employed potential mitigation procedures, are described in Chabreck (1968), Herke (1968, 1979), Baumannn and DeLaune (1982), Chabreck and Linscombe (1982), Boesch et al. (1984), Gosselink (1984), Rogers and Herke (1985a), Herke et al. (1987a), Walker et al. (1987), and Cowan et al. (1988).

Fixed-crest weirs are a common kind of water control structure. They have been constructed in Louisiana coastal marsh channels to reduce fluctuations in water levels and salinities and thereby enhance production of submerged aquatic vegetation for waterfowl (Chabreck 1968). Weirs are solid barriers with their crests usually set at least 15 cm below average marsh ground level. Free water movement occurs over the weir until the seaward water level recedes below the crest.

At this point, outflow continues until the water on the landward side reaches crest level, when the area is impounded; thus Herke (1971) referred to the areas landward of weirs as semi-impounded.

Zein-Eldin and Renaud (1986) indicated that juvenile penaeid shrimp ecology in marshes was not well understood. Area of intertidal vegetation has been hypothesized as the primary determinant of penaeid shrimp production (Turner 1977). Vegetated marsh edges are also central to the relation between shrimp habitat and production (Kutkuhn 1966; Boesch and Turner 1984; Zimmerman and Minello 1984). However, results from previous work on the details of shrimp ecology in Louisiana marshes have often been confusing or nonexistent. As Odum (1984) pointed out, now is the time to bridge the gap between the laboratory and nature by conducting studies in semi-natural settings. To improve our understanding of juvenile shrimp ecology in the marsh, I tested hypotheses about juvenile shrimp growth, mortality, emigration patterns, rearing densities, and responses to environmental conditions, as well as how a fixed-crest weir might influence shrimp life history variables. Results from these studies should be incorporated in the design and management of structures to minimize adverse effects on shrimp abundance.

This dissertation is arranged into six chapters; general introduction, general methods, and four subject chapters. Work occurred on 1) brown shrimp mark and recapture studies, 2) white shrimp mark and recapture studies, 3) shrimp density studies, and 4) investigations of environmental effects on white shrimp emigration from the marsh. Each subject chapter contains introduction, methods, results, discussion, and conclusion sections

CHAPTER II. Study Site and General Methods

I worked in a brackish marsh along Grand Bayou, a tidal bayou that flows west into Calcasieu Lake, in southwest Louisiana (Figure 1). The mouth of Grand Bayou is approximately 20.5 km (by water) from Calcasieu Pass on the Gulf of Mexico. To reach the study area from the Gulf, postlarval and juvenile shrimp moved through Calcasieu Pass, Calcasieu Lake, and Grand Bayou.

The study site consisted of two nearly identical, 35-hectare areas, one weired and the other unweired. About 75% of each was open water and about 25% was marsh vegetated primarily by *Spartina patens*. Levees built around a former natural marsh pond limited water exchange with Grand Bayou to identical, artificial chutes (Figure 2). Deflecting screens and traps (made of market grade monel wire cloth, with 4 x 4 mesh (per inch), 1.2-mm diameter wire, with 5.2-mm openings) were installed in each chute. Organisms entered the ponds by either passing through the mesh of the screens and traps or through a baffled, vertical slot, 7.6-cm wide, at the pondward end of the deflecting screens. Emigrating organisms were deflected past the vertical slot; all those too large to pass through the mesh were captured in identical traps (Figure 3).

In one chute, stop-logs formed a standard, fixed-crest weir, the crest of which was 30 cm below the average marsh ground level (Herke et al. 1987a). The traps were fished continuously. After 1 year of trapping, the weir was removed from one chute and placed in the other for the second year. The traps were then fished continuously for a second year. The study site was part of the Cameron-Creole Watershed Study, a comprehensive project funded by the U.S. Soil Conservation

Service to determine the effects of weirs on marsh fisheries (Herke et al. 1987a,b).

All trap and/or trawl samples collected in this study were processed by the method of Herke et al. (1987b). Catches were held in ice-water slush until processing, usually on the same day. All penaeid shrimp in each catch were counted and lengths were measured in 5-mm categories. If the catch was too large to measure and/or enumerate in a reasonable time, subsampling techniques were employed to make estimates (Holden and Raitt 1974; Herke 1978; Herke et al. 1984a).

In this study, all statistical tests are considered significant if $P < 0.05$. Differences are highly significant if $P < 0.01$.

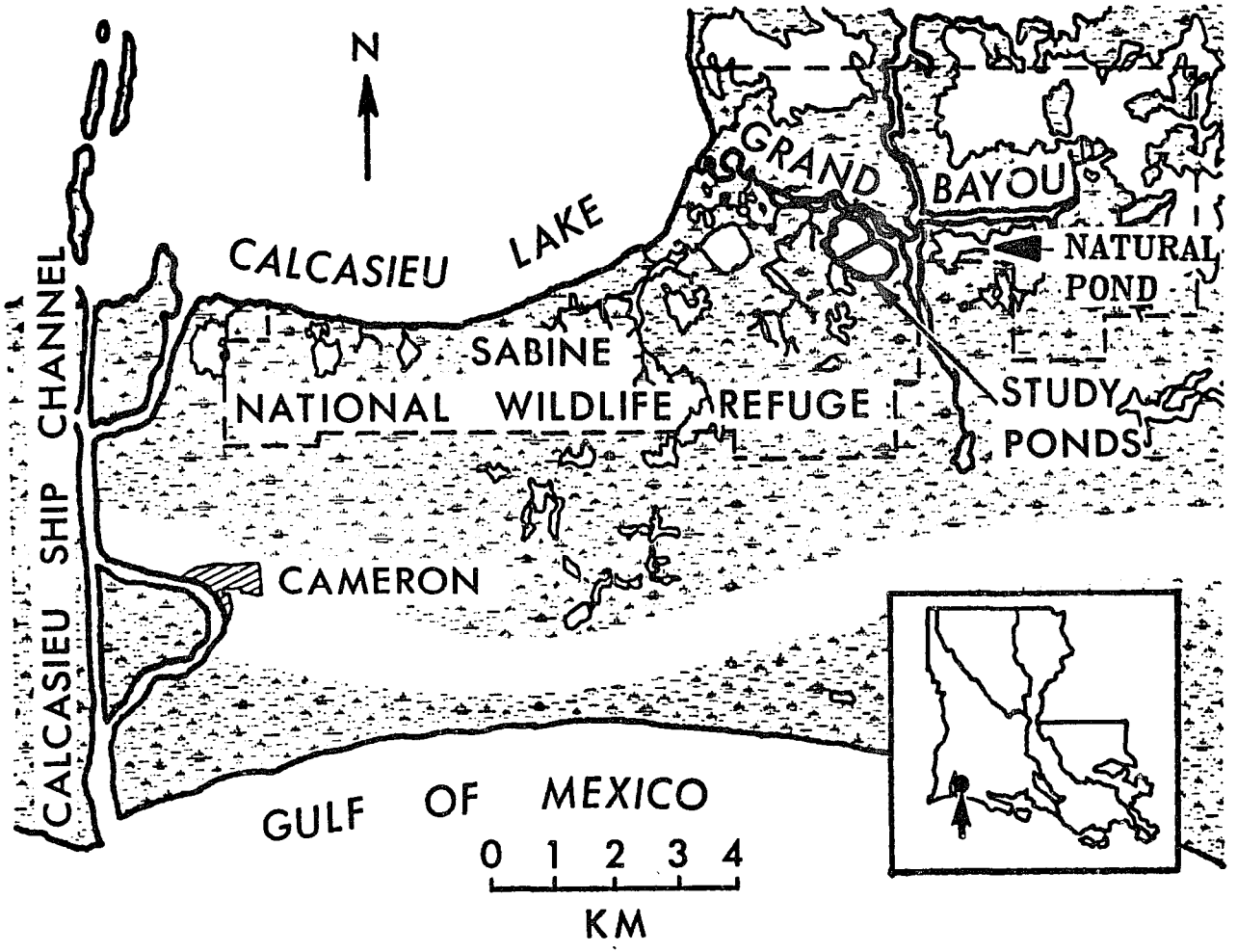


Figure 1. Location of study ponds, and nearby natural pond, relative to Lake Calcasieu and the Gulf of Mexico.

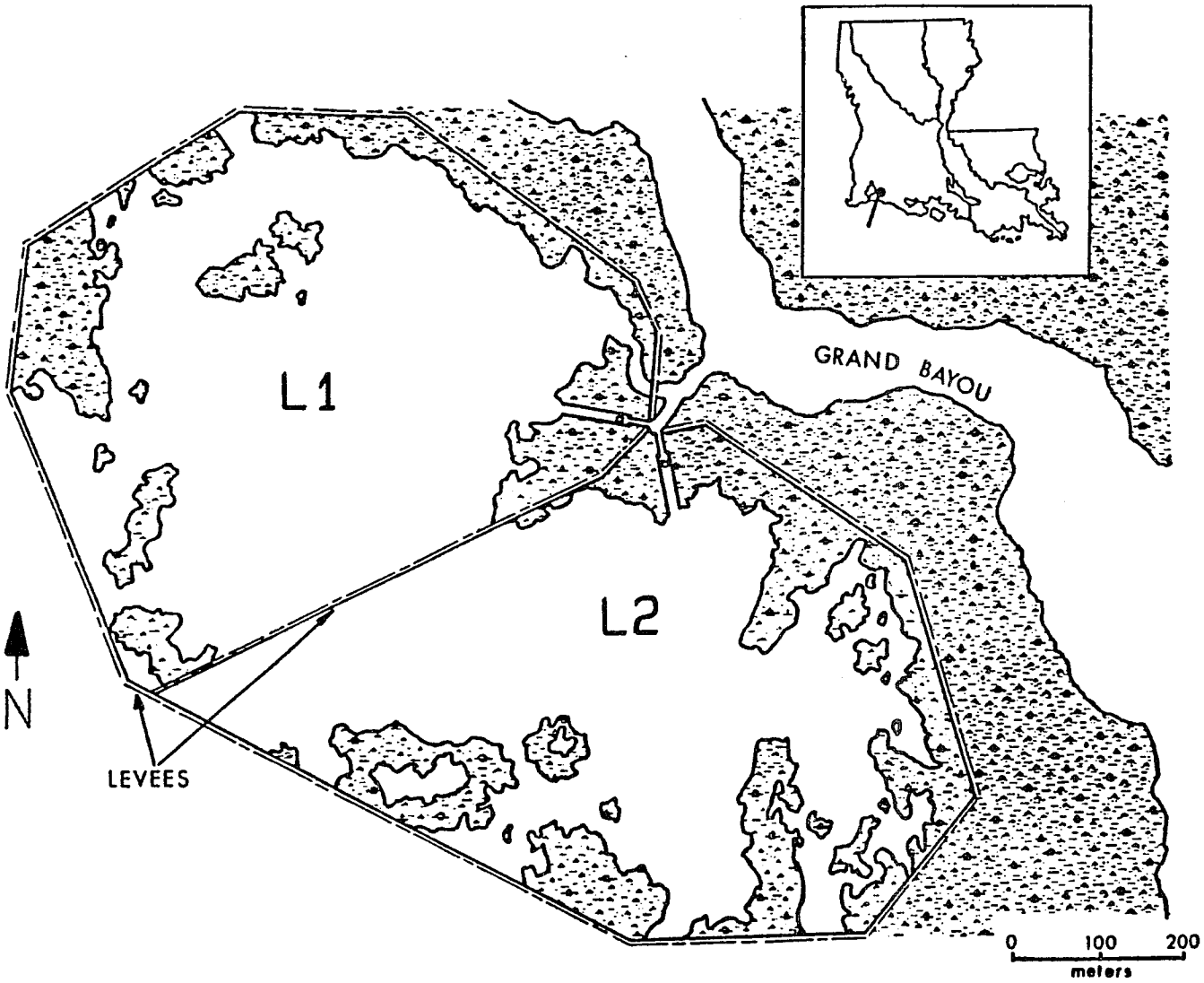


Figure 2. Arrangement of study ponds enclosed by low levees.

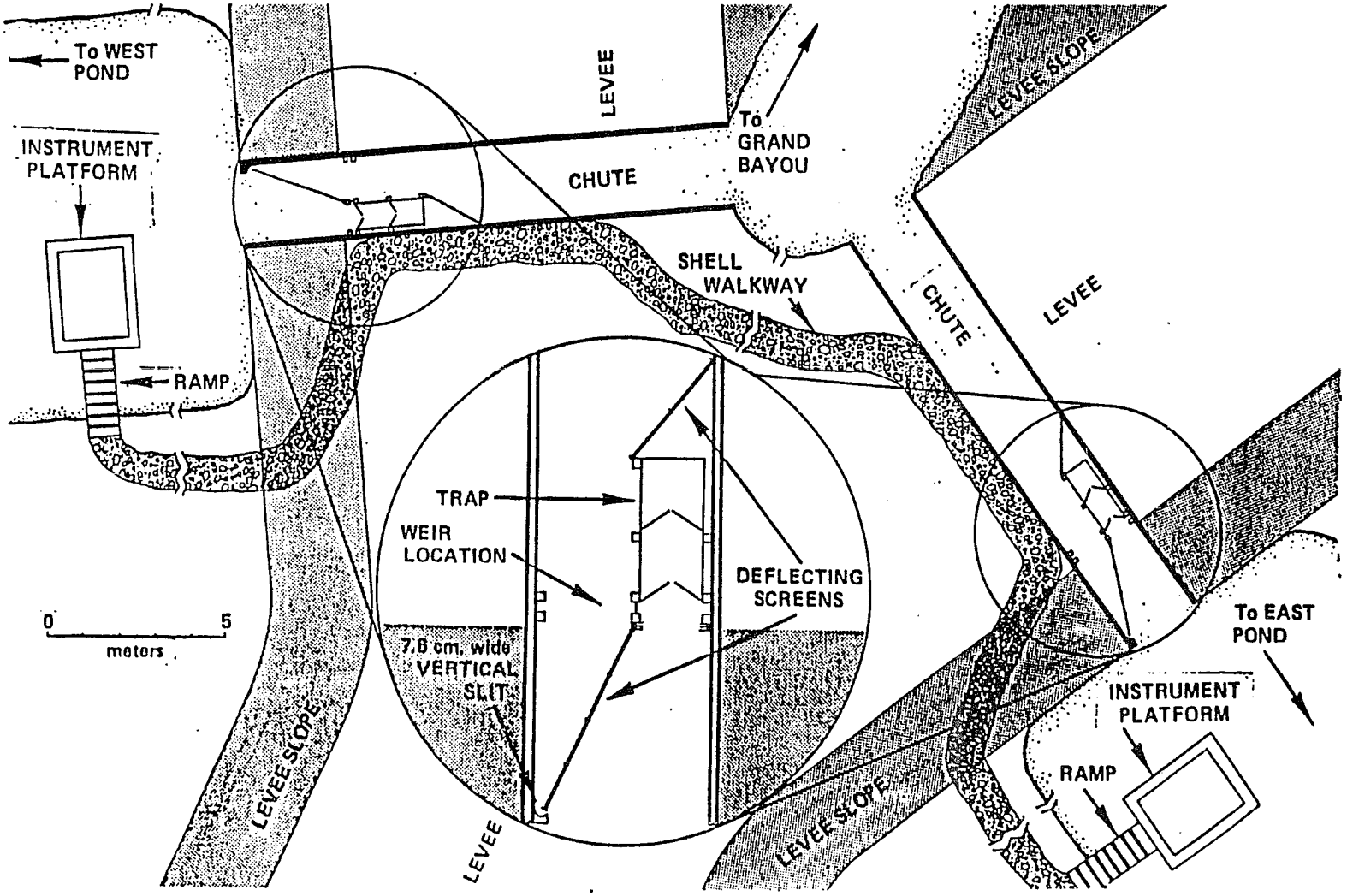


Figure 3. Details of identical chutes, deflecting screens, and traps at only entrance/exit to each pond. The weir was placed in one chute for the first year and switched to the other for the second year.

Chapter III. Effects of a fixed-crest weir on juvenile brown shrimp growth, mortality, and emigration.

Introduction

Brown shrimp *Penaeus aztecus* made up about half the 1989 U.S. Gulf of Mexico shrimp landings; their value was approximately $190 million (U.S. Department of Commerce 1990). Salt and brackish marshes along the Gulf are essential juvenile nurseries for brown shrimp (Kutkuhn 1966; Turner 1977; Zimmerman and Minello 1984). They spawn in the Gulf and their postlarvae and small juveniles are transported by currents to estuarine marshes from February to April (Gaidry and White 1973) where they grow rapidly along marsh edges (Boesch and Turner 1984; Zimmerman and Minello 1984). Several months later, juveniles migrate back to the Gulf (Gaidry and White 1973) where they spawn at the end of their first year.

Some aspects of brown shrimp ecology in Louisiana and Texas inshore waters have been extensively studied (see Zein-Eldin and Renaud, 1986, for review). In addition, several researchers have studied juvenile shrimp ecology in the shallowest water of interior salt and brackish marshes (e.g., Herke 1971; Rose et al. 1975; Knudsen et al. 1977; Perry 1981; Zimmerman and Minello 1984; Knudsen et al. 1985; Herke et al. 1987c). Some of the foregoing research occurred in areas influenced by weirs. Only Herke et al. (1987c) dealt with differences in shrimp growth and emigration between weired and natural marshes; they utilized otter trawling to reach their conclusions. No one has utilized a mark and recapture technique to compare shrimp growth and emigration, and no one has compared mortality, between

weired and natural marshes. The objective of this study was to determine the influence of a marsh weir on population attributes by recapturing marked shrimp as they emigrated from adjacent weired and unweired marsh ponds.

Methods

Brown shrimp were captured and marked in both ponds during May and June of 1983; marking methods were changed in 1984 because of experience from 1983 results. A double push trawl (Herke 1969) mounted on an airboat was used to collect shrimp. Total length (tip of rostrum to tip of telson) was measured to the nearest millimeter. Shrimp falling within specified length ranges were retained for marking. A relatively wide length range (45-55 mm) was marked in 1983 to maximize the number of recaptures. Because we were able to recapture a large percentage of those marked, we reduced the size range in 1984 (Table 1). Powdered fluorescent pigment (Scientific Marking Materials, Seattle, WA) and petroleum jelly were mixed together and injected into the shrimp's left side between the first and second abdominal segment; we used 3-cc disposable syringes with #25 X 5/8 needles (Klima 1965). Once marked, shrimp were observed in water-filled containers for a few minutes to determine whether they were injured. Any that were injured or seemed abnormal were destroyed; uninjured shrimp were counted and released into the pond from where they were captured. Six groups of shrimp, each distinctively marked with different colored pigments, were released in three paired groups with similar release lengths and times to compare growth, mortality, and emigration between weired and unweired ponds

(Table 1). Two other groups were released into the weired pond simultaneously in June, 1984, but at different mean lengths, to study differences in growth, mortality, and emigration of different-sized shrimp (Table 1).

All shrimp were captured as they emigrated from the two ponds (Herke et al. 1987a,b). Marked shrimp were recovered by examining all shrimp for marks under ultra-violet light. All undamaged, marked shrimp were measured. When total length could not be determined, because the shrimp was broken, the recapture was recorded but no length was assigned. These unmeasured recaptures were not used in growth calculations, but were included in emigration and mortality analyses.

Growth

Five models (simple linear, quadratic, linearized exponential, nonlinear exponential, and a von Bertalanffy growth function) were evaluated to determine which would provide the best description of brown shrimp growth rates. The simple linear model was rejected because it had unrealistic intercepts and plots of residuals indicated nonlinearity. The remaining four models were compared. I summed the corrected total sums of squares and summed the residual sums of squares over all release groups within a particular model and used these collective total and residual sums of squares to calculate a single R^2 for that model. The model resulting in the highest collective R^2 was chosen to best represent growth over all the experiments.

Table 1. Summary of brown shrimp releases and quadratic estimates of growth parameters for each release.

Release date(s)	Habitat	Marked shrimp released: Length (mm)	Marked shrimp released: N	Period of emigration	Total number recaptured	Results from quadratic models[a]: N[b]	R^2	a	b	c
17 May 1983	no weir	45-55	951	20 May - 27 Jul	432	239	0.62	6.23	0.59	-0.0003
18 May 1983	weir	45-55	598	20 May - 24 Jul	138	92	0.65	2.85	1.32	-0.0103
19 May 1983	no weir	45-55	1334	20 May - 25 Jul	619	318	0.72	4.12	0.70	-0.0015
20 May 1983	weir	45-55	363	24 May - 13 Jul	72	48	0.74	8.50	0.94	-0.0051
14-16 May 1984	weir	41-48	532	25 May - 21 Aug	184	177	0.87	0.86	1.48	-0.0074
17-18 May 1984	no weir	43-46	606	21 May - 27 Jul	188	156	0.89	-4.27	1.38	-0.0078
11, 13 Jun 1984	weir	82-85	501	12 Jun - 13 Sep	178	166	0.82	2.15	0.79	-0.0029
12 Jun 1984	weir	65-68	63	28 Jun - 21 Aug	36	35	0.81	1.99	1.33	-0.0072

[a] growth = a + b(days) + c(days)^2.

[b] only undamaged shrimp were used for growth calculations.

The quadratic model provided the best fit and was

$$\text{growth} = a + b(\text{days}) + c(\text{days})^2$$

where growth = length at recapture minus the midpoint of the length range at release and days = the number of days at large.

Weir effects on shrimp growth were evaluated by analysis of covariance (SAS PROC GLM, SAS Institute, Inc. 1988a) of the three release group pairs in which size and time of release were comparable between ponds. The model was

$$\text{growth} = \text{days} + \text{days}^2 + \text{pond} + \text{days*pond} + \text{days}^2\text{*pond}$$

where days^2 = a term describing the curvature of growth over time; pond = a class variable indicating weired or unweired; and days*pond and days^2*pond are terms to test for heterogeneity of the slopes (Freund and Littel 1981). The model for 1983 also included a term for the two release groups, i.e., the model was blocked on release date (Table 1). I used a similar model to compare growth rates between shrimp released simultaneously, but at different lengths, into the weired pond in 1984.

Mean lengths at emigration from the two ponds were calculated because the size at which shrimp enter Lake Calcasieu has direct fishery management implications. These lengths were not amenable to direct statistical comparison between ponds, however, because they were collected over different emigration periods (Table 1).

Relative mortality

Because all surviving brown shrimp emigrated from each pond and all surviving marked shrimp were captured and enumerated as they

emigrated, I computed monthly instantaneous mortality rates using the equation

$$Z = - \frac{\log_e(N_1/N_0)}{t}$$

(Gulland 1969), where Z = instantaneous total mortality rate, t = interval of time in months, N_0 = number released, and N_1 = number recaptured. Values for t were computed by dividing the mean number of days to recapture for each release group by the mean number of days in a month (30.42). Because there was no fishing in the study ponds, Z was an estimate of natural mortality. Z was not statistically compared between ponds because 1) Z has compound variance making testing an extremely complex statistical problem and 2) t varied over experiments, making comparisons of instantaneous mortality rates over different periods inappropriate.

Relative emigration patterns

Temporal emigration patterns of marked shrimp released at similar sizes and times in the two ponds were compared (PROC GLM, SAS Institute 1988a), to determine whether the weir influenced emigration. For 1983, the analysis of variance was blocked on release date (Table 1). To determine the effect of size on emigration, the emigration patterns of the two groups released at different mean lengths in the weired pond in June, 1984 were also compared.

Results

Growth

All surviving marked brown shrimp (about 35%) were recaptured as they emigrated. A few marked shrimp could have been lost to predators in the trap or missed during the examination for marks but I believe these losses were negligible. About 70% of the recaptured shrimp were undamaged and their lengths were utilized to generate growth functions (Table 1). The quadratic and nonlinear exponential models had the highest collective R^2 values (0.78), but the quadratic was chosen as the best model because the nonlinear exponential model provided less realistic intercepts for some release groups (Table 1).

Analysis of covariance of brown shrimp growth, with weir/no weir as the treatment and blocked on release date, for shrimp released in May, 1983 resulted in significantly different intercepts, by pond and release date, and significantly different curves for each pond but no difference in linear growth trends (Figure 4). Although linear growth was non-significant between ponds, the significantly different curvature indicated shrimp were growing faster in the weired pond for most of the time until emigration, especially in the earlier release group, but their growth slowed near the end (Figure 4). Furthermore, although the linear trends were similar for these two release groups, growth must have been faster in the weired pond because shrimp were released at the same size and time in the two ponds and the intercepts were significantly different between ponds (Figure 4). Growth rates ranged from 0.7 to 1.2 mm/d in the unweired pond and from 0.8 to 1.8 mm/d in the weired pond as estimated at 10 days after release and at the day of the last recapture from the 1983 growth curves in Figure 4.

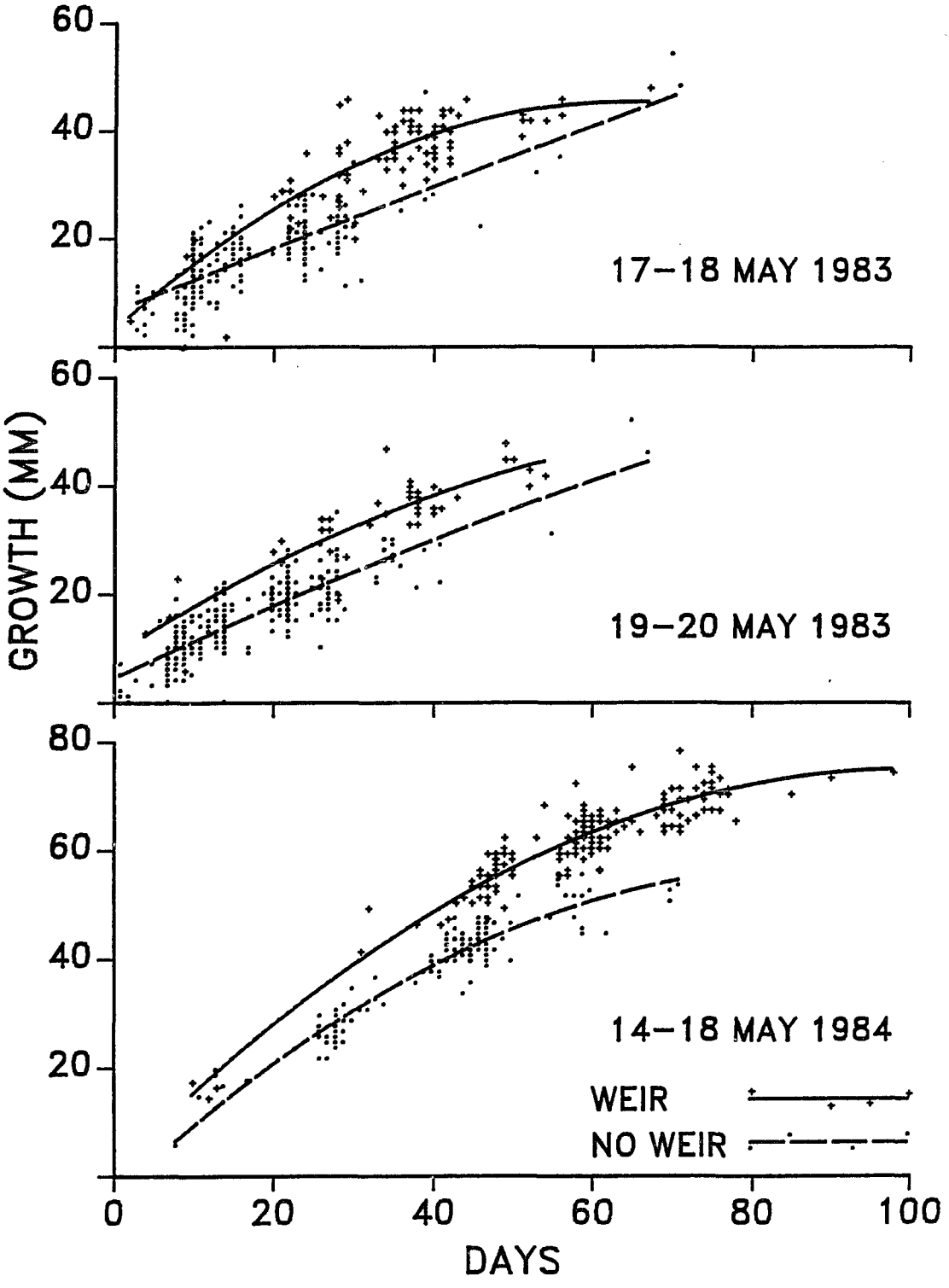


Figure 4. Quadratic growth of brown shrimp released simultaneously and at the same size in weired and unweired ponds (days = days since release).

(Estimates earlier than 10 days would be artificially high because the intercept from some of these models is extremely high.)

In 1984, brown shrimp grew faster in the weired pond than in the unweired pond; both the intercept and the linear trend were significantly different, although the curvature was not (Figure 4). As estimated from Figure 4, growth rates ranged from 0.8 to 1.0 mm/d in the unweired pond and from 0.8 to 1.6 mm/d in the weired pond.

Shrimp released at 65-68 mm in the weired pond grew significantly faster than shrimp released at 82-85 mm in the same pond (Figure 5). The linear trends were significantly different although the curvature was not. Based on estimation from Figure 5, growth ranged from 0.9 to 1.6 mm/d for shrimp released at 65-68 mm and from 0.5 to 1.0 for shrimp released at 82-85 mm.

Figures 4 and 5 illustrate brown shrimp growth in shallow marsh waters under a variety of conditions (different months, years, initial lengths, conditions of impoundment). Most previous growth estimates were reported in millimeters per day (see Knudsen et al. 1977, for a review). My estimates were similar to those using similar techniques.

Relative Mortality

Monthly instantaneous mortality rates differed between ponds and years (Table 2). For May releases, mortality was greater in the weired pond in 1983 but greater in the unweired pond in 1984. Mortality was less in both ponds in 1984 than in 1983 for shrimp released at about the same size in May of each year. Mortality was estimated to be 1.412-1.582 in the weired pond and 1.270-1.229 in the unweired pond in 1983 and 0.550 in the weired pond and 0.877 in the unweired pond in

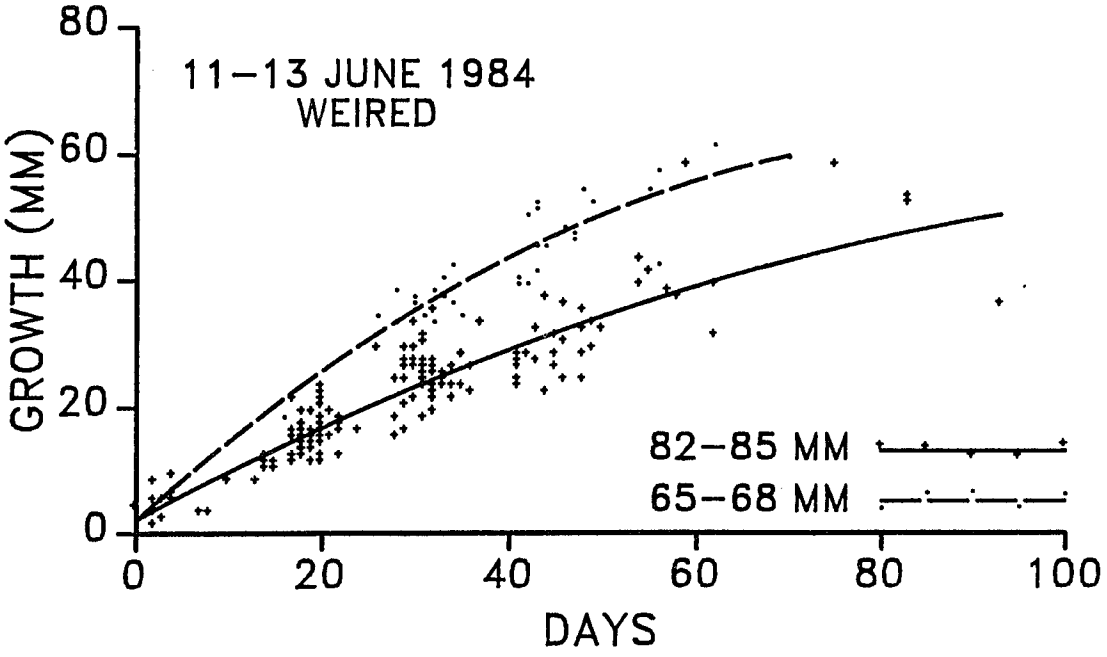


Figure 5. Quadratic growth of brown shrimp released simultaneously in the weired pond but at different initial lengths.

Table 2. Comparative brown shrimp monthly instantaneous mortality rates, mean time until emigration, and mean length at emigration between weired and unweired marsh ponds and between shrimp released at two sizes in the unweired pond.

	Monthly mortality		Mean residence time (days)			Mean length at emigration (mm)	
Release date(s)	Weired	Unweired	Weired	Unweired	t	Weired	Unweired
17, 18 May 1983	1.412	1.270	31.6	18.9	12.4**	84.8	66.5
19, 20 May 1983	1.582	1.229	31.1	19.0	8.9**	83.4	66.1
14-18 May 1984	0.550	0.877	58.7	40.6	13.0**	106.1	83.5
Size at release:	Larger	Smaller	Larger	Smaller	t	Larger	Smaller
11-13 Jun 1984	1.097	0.421	28.7	40.4	-4.1**	105.4	109.7

** $P < 0.01$

1984. Although Herke et al. (1987a,b) captured all nekton emigrating from the study ponds, I was unable to estimate the proportion of brown shrimp mortality resulting from predation.

Of the two groups released simultaneously but at different sizes in the weired pond, estimated mortality was greater for larger shrimp (1.097) than for smaller shrimp (0.421) (Table 2). These experiments were conducted in the weired pond where there is a delay in emigration relative to the unweired pond (described below). Perhaps the mortality rate was greater for shrimp whose emigration in response to physiologically-based stimuli is delayed.

My estimated instantaneous monthly mortality rates (0.55-1.58) were much greater than those calculated for larger brown shrimp (0.15 per month) by Parrack (1981), who used mark and recapture data, and Nichols (1984), who used catch and effort data (0.28 per month). This difference is likely due to a general decrease in mortality in the more stable Gulf environment where the shrimp are also larger. Wide mortality variation in my study generally indicates that natural mortality in marsh nurseries may depend on a variety of variables not necessarily related to semi-impoundment.

Some of the mortality in this study could have been due to the handling and marking of shrimp. However, tests of the method by Klima (1965) and Knudsen et al. (1977) indicated survival of marked shrimp was not different from unmarked shrimp.

Relative Emigration Patterns

Among equal-sized shrimp marked at about the same time, emigration occurred earlier at the unweired than at the weired pond

(Figure 6). Shrimp remained significantly longer in the weired pond in both years (Table 2). Mean time to emigration was estimated to be 31.1-31.6 d in the weired pond and 18.9-19.0 d in the unweired pond (Table 2).

On the average, of the two groups released in the weired pond in June, 1984, the 65-68-mm group emigrated significantly later (11.7 d) than the 82-85-mm group (Table 2, Figure 5). Parker (1970) and Gaidry and White (1973) also found that emigration from the marsh is partly size-dependent. Herke (1971, 1977) stated that emigration is a "bleeding-off" of larger individuals.

Peaks in emigration were related to occurrence of both new and full moons (Figure 6). The phenomenon of delay appears to have been superimposed on the lunar effect in the weired pond because emigration occurred in conjunction with a new or full moon even though it was later than from the unweired pond. These semi-monthly peaks in emigration were even more obvious for the total brown shrimp catch (marked plus unmarked; Herke et al. 1987a).

Length at emigration

Mean length of marked shrimp at emigration (not to be confused with growth) was greater in the weired pond (Table 2). On any given day, the average size of all brown shrimp (marked and unmarked) migrating from the weired pond was also larger than of shrimp moving from the unweired pond (Herke et al. 1987a). Although growth in some tests was faster in the weired pond, the delay in emigration was likely another important cause of the larger size of shrimp from the weired pond. Hence, the lengths in Table 2 do not alone necessarily

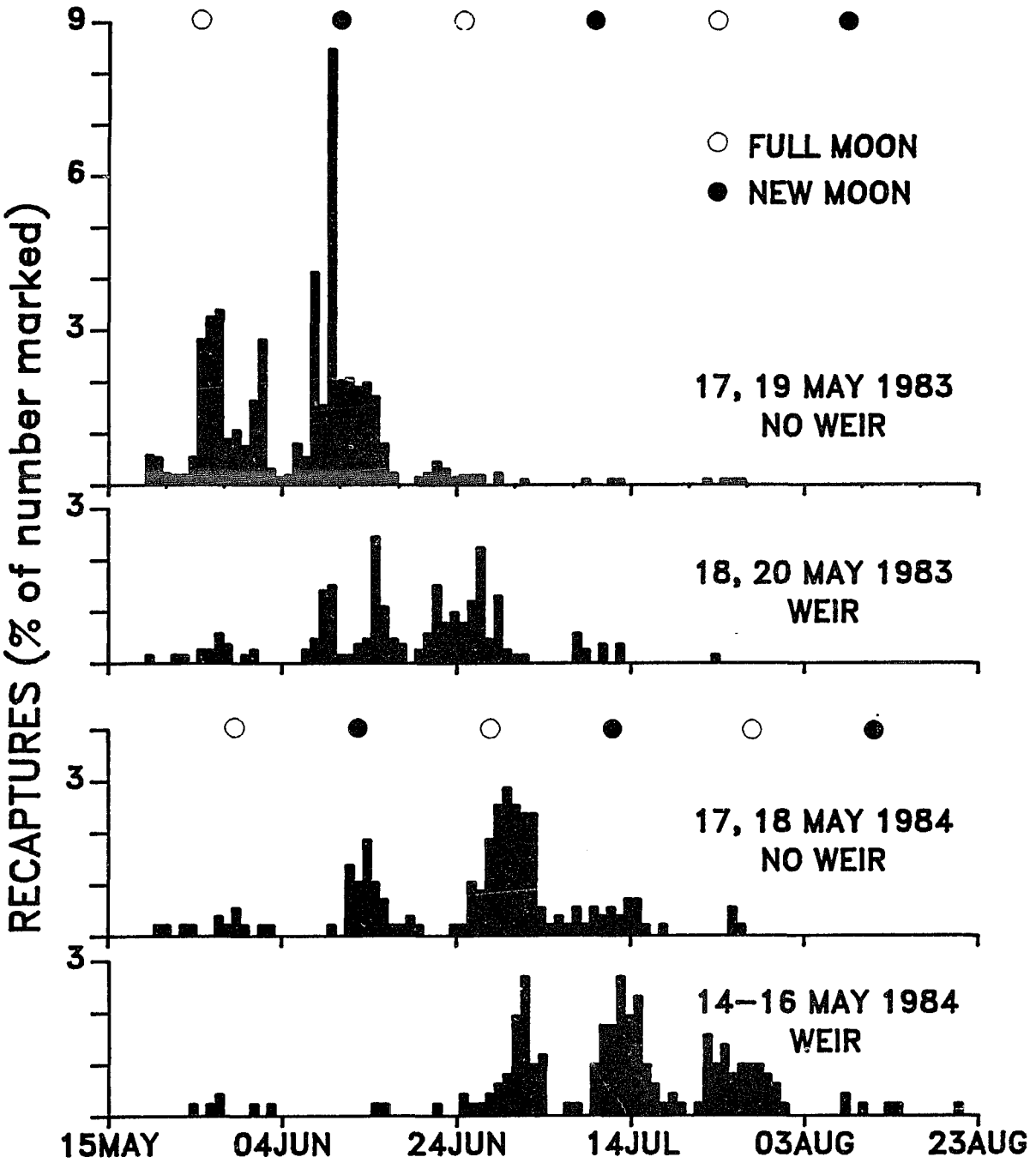


Figure 6. Emigration patterns of brown shrimp marked and released in May of 1983 and 1984 in weired and unweired marsh ponds.

indicate better conditions for shrimp growth in the weired pond.

The mean length at emigration varied between years (Table 2). It was estimated to be 83.4-84.8 mm from the weired pond and 66.1-66.5 from the unweired pond in 1983 and 106.1 from the weired pond and 83.5 from the unweired pond in 1984. Shrimp marked and released at a slightly smaller average length in May 1984 (compared with 1983) emigrated at a larger mean length. Because brown shrimp in this area migrate directly from shallow marshes to the fishing area (Knudsen et al. 1985), the length at emigration from the ponds is essentially the length of recruits to the fishery.

The observed difference in mean length at emigration for shrimp released at two different sizes in the weired pond in 1984 was 4.3 mm (Table 2). Shrimp that were smaller at release emigrated significantly later and were slightly larger at emigration. This again supports the theory of "bleeding off" (Herke 1971,1977).

Discussion

Shrimp grew somewhat faster in the weired ponds. The weir affected the abundance of emigrating shrimp and their length at emigration; fewer but larger shrimp emigrated from the weired than from the unweired pond on any given day (Herke et al. 1987a). Perhaps these differences were due to different immigration patterns between ponds. In a simultaneous study, Bradshaw (1985) captured 26% (1983) and 83% (1984) fewer postlarval and small juvenile brown shrimp in the weired than in the unweired pond. Lower densities of shrimp in the weired pond (Bradshaw 1985; Chapter V) could have reduced intraspecific competition, thereby increasing growth. It is difficult,

therefore, to conclude the weir, per se, was associated with increased growth although there could have been an indirect association.

There may be two sources of slight error in brown shrimp growth models generated from regression of increase in length of recaptured emigrants over time. One is that initial size of shrimp at release is not used in the model; it is based only on the lengths of those recaptured. Thus, the slope could have been biased downward, depending on the distribution of the observations, due to natural growth slowing with age (perhaps using shrimp of equal initial length or forcing the regression through the origin would reduce this effect).

The other possible source of error may have resulted from the method of recapture--taking marked shrimp as they emigrated past a single point. Herke (1971, 1977) and Wicker et al. (1988) concluded that brown shrimp emigration from the marsh is a "bleeding-off" of larger individuals and the same phenomenon was also noted in this study. Thus, fast-growing individuals should emigrate earlier than the slow-growing ones. The resultant effect on the regression models may have been to bias the first values upward and the later values downward, relative to average growth. Thus, I may have slightly underestimated the growth rate of later emigrating shrimp and overestimated the growth rate of earlier emigrating shrimp.

There is a possibility that growth rate estimates were influenced by loss of marked shrimp to predation within the traps. However, the only negative effect on growth studies would have been a bias caused by predation differences between larger or smaller shrimp, or between traps in the case of the weir-no weir comparison. Since the traps were

emptied every 24 h, and unmarked shrimp greatly outnumbered marked shrimp in the trap, I believe this bias would have been negligible.

Shrimp were larger and emigrated later from the weired pond; their greater length at emigration was explained partly by faster growth and partly by the delay in emigration. The delay may have been caused by reduced fluctuations in environmental conditions (as hypothesized by Herke 1971, 1977), by improved habitat and/or reduced intraspecific competition in the weired pond, or by the physical barrier presented by the weir. However, faster growth rates in the weired pond (in some cases) may be an indication that the delay was caused, at least partially, by improved habitat or reduced intraspecific competition.

Shrimp mean lengths were greater and emigration was later in 1984 than in 1983 (Table 2), for groups released at similar sizes in May of each year. This supports the hypothesis that shrimp may respond to certain external stimuli for emigration (Herke 1971) and verifies that size at emigration may differ annually (Parker 1970).

Shrimp emigration from both weired and unweired ponds was associated with new and full moons, even though emigration from the weired pond was delayed. This lunar relationship has also been noted during other brown shrimp emigration studies (e.g., Copeland 1965; King 1971; Rose et al. 1975; Capone 1984; and Knudsen 1986) although Copeland (1965) concluded that emigration peaked only during the full moon and King (1971) concluded that it peaked during the new moon only.

The total catch, by weight, of all emigrating brown shrimp (marked and unmarked) was 100 and 118% greater from the unweired than the weired pond in 1983 and 1984, respectively (Herke et al. 1987a).

Thus, although the weired pond produced larger and somewhat faster-growing shrimp in both years, the unweired pond produced much more shrimp biomass. Investigations of optimum juvenile shrimp densities in relation to growth rate and total biomass production in coastal marshes are desirable in the future.

The question arises whether the economic value of larger emigrants from the weired area offsets the value of reduced total biomass produced there when the shrimp are eventually harvested. The relative contribution to the fishery by shrimp from each pond relates to this question. I used data from Herke et al. (1987b) and summarized total export of brown shrimp from both ponds and overall mean lengths of all brown shrimp emigrants (Table 3). Assuming the length attained by shrimp emigrating from the weired pond was more desirable to the fishery, the growth necessary for shrimp from the unweired pond to reach that size can be obtained by subtraction; it was 11 mm in 1983 and 18.3 mm in 1984. Since growth rate late in the emigration period was about 0.67 mm/d in 1983 and about 0.81 mm/d in 1984 (Figure 4), shrimp from the unweired pond would have required about 16.4 additional days in 1983, and 22.6 in 1984, to attain a size equivalent to shrimp emigrating from the weired pond. During the same period, shrimp were subject to daily instantaneous mortality--0.041 in 1983 and 0.029 in 1984 (mean monthly unweired-pond mortality from Table 2 divided by 30.42). I used the mortality equation

$$N_t = N_o \, e^{-Zt}$$

(Ricker 1975) to estimate that 161,631 and 148,604 shrimp from the

Table 3. Total export and mean lengths of all brown shrimp emigrating from weired and unweired ponds in 1983 and 1984 (from Herke et al. 1987a,b).

Pond	Mean length (mm)	Total export	
		Biomass (g)	Numbers
	1983		
Weir	95.0	419,635	101,345
No weir	84.0	839,706	316,475
	1984		
Weir	99.5	392,748	57,370
No weir	81.2	857,794	286,064

unweired pond would have survived to attain a size equivalent to those from the weired pond in 1983 and 1984, respectively. These totals were 59 and 159% greater, in numbers of equal-sized shrimp, than the production from the weired pond in 1983 and 1984 (Table 3). Because the shrimp fishery operated just downstream of the study area, and shrimp moved directly downstream after emigration from shallow marsh ponds (Knudsen et al. 1985), many small shrimp probably were, and continue to be, caught before they grow to a size equal to that of shrimp leaving the weired pond. Whether the many smaller shrimp from unimpounded areas are caught almost immediately or allowed more time to grow, natural areas apparently contribute more biomass per hectare to shrimp harvests than do weired areas.

Shrimp released about the same time in May of 1983 and 1984 remained in both ponds longer, and mortality was lower, in 1984 than in 1983. This may have been due to reduced intraspecific competition because of the lower overall abundance of shrimp in 1984 (Table 3) (Herke et al. 1987a; Chapter V), or possibly to better environmental conditions for shrimp in 1984.

Instantaneous shrimp mortality was variable during our study and the influence of the weir on mortality was unclear. Predation on shrimp is important in marsh nurseries (Minello et al. 1987). Influences of the weir on densities of both shrimp and predators probably further obscured any patterns of mortality that occurred. Perhaps future investigations can be focused on the relation between weirs, predators, and mortality. Also, future investigators may want to determine whether mortality subsequent to emigration from interior marshes varies annually, as it may within the marsh nursery.

Mortality was highest in the same pond in both years (the weir was switched between ponds for the second year). The same pond had consistently greater mortality on white shrimp as well (Chapter IV). The only noticeable difference between the two ponds was that the one with greater mortality had an average depth of 43 cm and the average depth of the other was 47 cm.

While larger shrimp emigrating from marshes behind weirs are an attractive benefit of weirs, the overall reduction in shrimp production mandates extreme care in decisions to construct weirs. The foregoing results support the idea that weir installation and operation should be conducted on a case by case basis (Rogers and Herke 1985a). It is becoming more apparent that standard, fixed-crest weirs are detrimental to shrimp production. Thus alternatives, such as 1) different structure design, 2) structures having operational flexibility, or 3) no weir installation, should be explored and applied in marshes known to be shrimp nurseries.

Conclusions

1. Brown shrimp growth was faster in the weired pond in both years.
2. Shrimp released at 65-68 mm in the weired pond grew faster than shrimp released at 82-85 mm in the same pond.
3. Monthly instantaneous mortality was variable between ponds and years; no conclusions could be made regarding the effect of the weir on mortality.

4. Monthly instantaneous mortality ranged from 0.55 to 1.58 in the weired pond and 0.88 to 1.27 in the unweired pond. These values were substantially greater than mortality estimates for older and larger shrimp in the Gulf.
5. Brown shrimp marked and released at similar sizes and times emigrated from weired ponds significantly later (12-18d) than from unweired ponds.
6. Of brown shrimp released simultaneously but at different sizes, the larger shrimp emigrated significantly earlier; this supports the hypothesis that emigration is a "bleeding-off" of larger individuals.
7. Timing of brown shrimp emigration was related to both new and full moons regardless of size or pond type.
8. Mean total length of marked shrimp at emigration ranged from 83 to 106 mm for the weired pond and from 66 to 84 mm for the unweired pond.
9. Even though brown shrimp emigrating from the weired pond were larger, concurrent research demonstrated that total biomass of all brown shrimp emigrating from the unweired pond was more than double the biomass from the weired pond.

CHAPTER IV. Effects of a fixed-crest weir on juvenile white shrimp mortality, growth, and emigration.

Introduction

Most young white shrimp are carried into marshes on flood tides as postlarvae or small juveniles in summer and early fall (Gaidry and White 1973). They move into upper reaches of the coastal marshes and remain until emigration, which proceeds gradually at first and then in pulses stimulated by sharp declines in temperature through the fall according Lindner and Anderson (1956), Gaidry and White (1973), and Rogers and Herke (1985a). Most white shrimp are normally gone from Gulf coastal marshes by the end of December (Rogers and Herke 1985b; Herke et al. 1987c).

Documentation of shrimp growth, mortality, and migration patterns have been cited as research priorities for improved management of shrimp resources (Powers 1984). Zein-Eldin and Renaud (1986) also indicated that human understanding of juvenile white shrimp ecology in marshes was limited. Water control structures constructed in marsh waterways likely affect white shrimp ecology as they do for brown shrimp (Knudsen et al. 1989). These effects should be considered in the design and management of structures so that losses to shrimp production can be minimized. Therefore, I studied growth, mortality, and emigration patterns of juvenile white shrimp by releasing marked shrimp in two shallow marsh ponds, one with a weir at its only exit and the other without a weir. All surviving marked shrimp were later recaptured as they emigrated toward the Gulf of Mexico.

Methods

Mark/recapture experiments were performed in 1983 and 1984; timing of shrimp releases varied between years. A double push trawl (Herke 1969) mounted on an airboat was used to collect shrimp from the study ponds. After fishing about 3 min, the white shrimp were quickly measured (total length) and those of appropriate size were retained in water-filled containers. Powdered fluorescent pigment (Scientific Marking Materials, Inc., Seattle, WA) was mixed with petroleum jelly and injected into the shrimp's left side between the first and second abdominal segments with Stylex 3-cc disposable syringes with #25 X 5/8 needles (Klima 1965). This marking technique does not cause significant marking mortality (Klima 1965; Clark and Caillouet 1973; Knudsen et al. 1977). We observed marked shrimp for several minutes and injured or abnormal shrimp were destroyed. Remaining shrimp were counted and released into the study ponds (Figure 2).

Twelve marked groups, differentiated by their pigment colors, were released over the two years. In 1983, three groups of 45-55-mm (TL) shrimp were released in each pond between 6 September and 19 October (Table 4). On August 28 and 29, 1984, three groups of shrimp, 49, 59, and 68 mm long, were released in each pond (Table 4).

Marked shrimp were recovered by continously trapping all nekton emigrating from each pond (Herke et al. 1987a,b) and examining shrimp under ultra-violet light. Total length and recovery location were recorded for each undamaged, recaptured shrimp. When damage precluded total length measurement, the return was noted but no length was assigned. Data from these unmeasured returns were not used in growth calculations, but were included in emigration and mortality analyses.

Table 4. Dates, lengths, and number of white shrimp released and recaptured, relative times to emigration, and mortality rates in ponds with and without weirs.

Date released		Length	Number released		Number recaptured		Mean time to emigration (days)			Monthly Z	
No weir	Weir	(mm)	No weir	Weir	No weir	Weir	No weir	Weir	t	No weir	Weir
					1983						
Sep 6-7	Sep 12-14	45-55	1223	728	424	71	43.2	50.0	-3.01**	0.76	1.45
Sep 19-21	Sep 26-27	45-55	600	510	159	78	47.4	37.6	5.03**	0.87	1.55
Oct 11-12	Oct 17-19	45-55	1243	1057	347	140	34.9	30.2	5.11**	1.13	2.08
					1984						
Aug 29	Aug 28	49	200	74	24	14	44.1	59.9	2.47*	1.46	0.86
Aug 29	Aug 28	59	138	89	24	12	31.5	40.4	1.17	1.72	1.54
Aug 29	Aug 28	68	84	55	10	9	42.8	45.5	0.35	1.54	1.16

* $P < 0.05$

** $P < 0.01$

Mortality

The ratio of the number of shrimp released to the number recaptured provided an overall mortality estimate from release to recapture at emigration. Since all emigrating shrimp, both marked and unmarked, were captured, the entire population of white shrimp surviving until the time of emigration was enumerated and did not need to be estimated. Mark/recapture data were used to estimate instantaneous monthly mortality expressed as

$$Z = \frac{\log (N_0 / N_1)}{t},$$

(Gulland 1969) where Z is the instantaneous total mortality coefficient, t is the interval of time at liberty (in months), N_0 equals the number released, and N_1 is the number recaptured. Monthly values of t were computed by dividing the mean number of days at liberty by 30.4 (average days/month). Since there was no fishing in our study ponds, Z was an estimate of natural mortality. Z was not statistically compared between ponds because 1) Z has compound variance making testing an extremely complex statistical problem and 2) t varied over experiments, making comparisons of instantaneous mortality rates over different periods inappropriate.

Growth

Five models (simple linear, quadratic, linearized exponential, nonlinear exponential, and a von Bertalanffy growth function) were evaluated for their ability to estimate shrimp growth determined from the mark and recapture data. The simple linear model was rejected

because it had unrealistic intercepts and examination of the residuals indicated nonlinearity. Each of the remaining models was then evaluated relative to the others. I summed the corrected total sums of squares over all release groups, summed the residual sums of squares over all release groups, and used these collective total and residual sums of squares to calculate a single r^2 for each model. The linearized exponential model had the highest collective r^2 values for both 1983 and 1984 data. The original model form was

$$\text{growth} = a * (\text{days}^b)$$

where growth equals increase in length at recapture and days are the number of days between release and recapture. The model was linearized as

$$\ln(\text{growth}) = \ln(a) + b(\ln[\text{days}]).$$

This model was the best expression of growth for a single release group.

I used analysis of covariance to compare growth between ponds (PROC GLM, SAS Institute, Inc. 1985) applied to the six experimental pairs; shrimp length and time of release were comparable between ponds for each pair. The basic linearized SAS ANCOVA model was

$$\ln(\text{growth}) = \text{pond} + \ln(\text{days}) + \text{pond}*\ln(\text{days})$$

where ln(growth) is the natural log of change in length between release and recapture, pond is a class variable indicating weir or no weir, ln(days) is the natural log of the number of days (+1) between release and recapture, and pond*ln(days) = an interaction term to test

heterogeneity of the two slopes (Freund and Littel 1981). Plots of these six pairs of release groups were also prepared.

In 1983, the pairs of marked shrimp groups were released at three times over the fall (Table 4). Because I wanted to test the effect of release time, as well as the weir effect, the analysis of covariance model contained terms for time. It was

$$\ln(\text{growth}) = \ln(\text{days}) + \text{pond} + \text{reltime} + \text{pond*reltime} + \text{pond*ln(days)} + \text{reltime*ln(days)} + \text{pond*reltime*ln(days)}$$

where reltime represented release in early September, late September, or October (Table 4).

In 1984, the pairs of marked shrimp groups were released at three lengths but at the same time (Table 4). Because I wanted to test the effect of release size, as well as the weir effect, the analysis of covariance model contained terms for release length. It was

$$\ln(\text{growth}) = \ln(\text{days}) + \text{pond} + \text{length} + \text{pond*length} + \text{pond*ln(days)} + \text{length*ln(days)} + \text{pond*length*ln(days)}$$

where length represents 49, 59, or 68 mm (Table 4).

Because in 1984 all shrimp were released at specific lengths rather than length ranges, estimates of 1984 growth rates were also made by simply subtracting length at release from length at recapture. These growth increments were then compared in t tests to determine the effects of the weir and length at release on growth.

Emigration

I used all recovered marked shrimp to generate histograms of daily recaptures (as a percent of the number released) in each emigration trap. Histograms for each year were evaluated for emigration patterns 1) between ponds with and without a weir, 2) between shrimp released at the same length but at different times (1983), and 3) between shrimp released simultaneously but at different lengths (1984). Lunar phases were noted on the histograms. Additional histograms, comparing all recaptures from a single pond with daily air temperature, were also evaluated. The number of days until marked shrimp emigrated was analyzed with analysis of variance (PROC GLM, SAS Institute 1988a) with ponds as a treatment in both years, release time as a treatment in 1983, and release length as a treatment in 1984.

Results

Mortality

Instantaneous monthly mortality ranged from 0.76 to 2.08 in the study ponds (Table 4). Mortality was greater in the pond with the weir in 1983. However, because shrimp were consistently released later in the weired pond (Table 4), and because mortality apparently increased as autumn progressed, the relative difference in mortality between ponds might not have been as great as it appeared. The general increase in mortality for groups released progressively later in 1983 (Table 4) may have been due to the onset of cooler weather.

Mortality was consistently greater in the pond without a weir in 1984 (Table 4). This perhaps resulted from higher densities of shrimp there than in the weired pond, as reported in Chapter V and also

indicated by total trap catches of Herke et al. (1987a). However, 1983 white shrimp densities were greatest in the unweired pond (Chapter V; Herke et al. 1987a) and mortalities were less there than in the weired pond. Some clues regarding observed mortality patterns may be offered by a consistent pattern of highest mortalities always occurring in the east study pond, regardless of whether it had a weir on it, and regardless of shrimp species (Tables 2 and 4). The only notable physical difference between the ponds was that average depth in the east pond was 43 cm while the west pond averaged 47 cm (Herke et al. 1987b). I reviewed predator catches by Herke et al. (1987b) and found no particular concentration of predators in that pond.

There was no apparent effect of length on observed mortality rates. Shrimp released simultaneously but at different lengths in 1984 did not appear to differ in mortality in either pond (Table 4).

Monthly Z values ranged from 0.86 to 2.08 in the pond with a weir and from 0.76 to 1.72 in the pond with no weir (Table 4). These monthly mortality rates were much higher than those reported for commercial-sized Gulf of Mexico white shrimp (Powers 1984). Smaller shrimp are likely more susceptible to factors such as environmental fluctuations, competition, and predation in the marsh.

Growth

There were significant interactions in the 1983 full analysis of covariance model with pond type and release times as treatments (Table 5). This meant the relation of growth between ponds varied over release times (Table 5, Figure 7). Because of the interactions, I performed a separate analysis of covariance for each release period

Table 5. Analysis of covariance of the natural log of shrimp growth (+1) over the natural log of days until recapture (+1) with ponds (weir and no weir) as a treatment in all models. The full models also contain release date and release size as treatments in 1983 and 1984, respectively.

Release date(s)	Release length	Model terms	Type I sums of squares	Pr > F
		1983 - Full model		
6 Sep - 19 Oct	45-55	Ln(days)	177.19	0.0001
		Pond	32.78	0.0001
		Reltime	92.79	0.0001
		Pond*reltime	1.31	0.0012
		Ln(days)*pond	0.01	0.7548
		Ln(days)*reltime	3.38	0.0001
		Ln(days)*pond*reltime	0.53	0.0632
		1983 - Separate models		
6-14 Sep	45-55	Pond	22.34	0.0001
		Ln(days)	145.46	0.0001
		Ln(days)*pond	0.52	0.0227
19-29 Sep	45-55	Pond	9.69	0.0001
		Ln(days)	5.33	0.0001
		Ln(days)*pond	0.06	0.3676
11-19 Oct	45-55	Pond	10.91	0.0001
		Ln(days)	20.89	0.0001
		Ln(days)*pond	0.17	0.2951

continued.

Table 5. Continued.

Release date(s)	Release length	Model terms	Type I sums of squares	Pr > F
		1984 - Full model		
28-29 Aug	49,59,68	Ln(days)	27.71	0.0001
		Pond	3.59	0.0001
		Relsize	0.98	0.0005
		Pond*relsize	0.02	0.8221
		Ln(days)*pond	1.12	0.2932
		Ln(days)*relsize	0.74	0.0029
		Ln(days)*pond*relsize	0.35	0.0574
		1984 - Separate models		
28-29 Aug	49	Pond	4.24	0.0001
		Ln(days)	2.83	0.0001
		Ln(days)*pond	0.03	0.3468
28-29 Aug	59	Pond	2.32	0.0001
		Ln(days)	7.95	0.0001
		Ln(days)*pond	0.06	0.4197
28-29 Aug	68	Pond	0.52	0.0618
		Ln(days)	6.32	0.0001
		Ln(days)*pond	0.40	0.0985

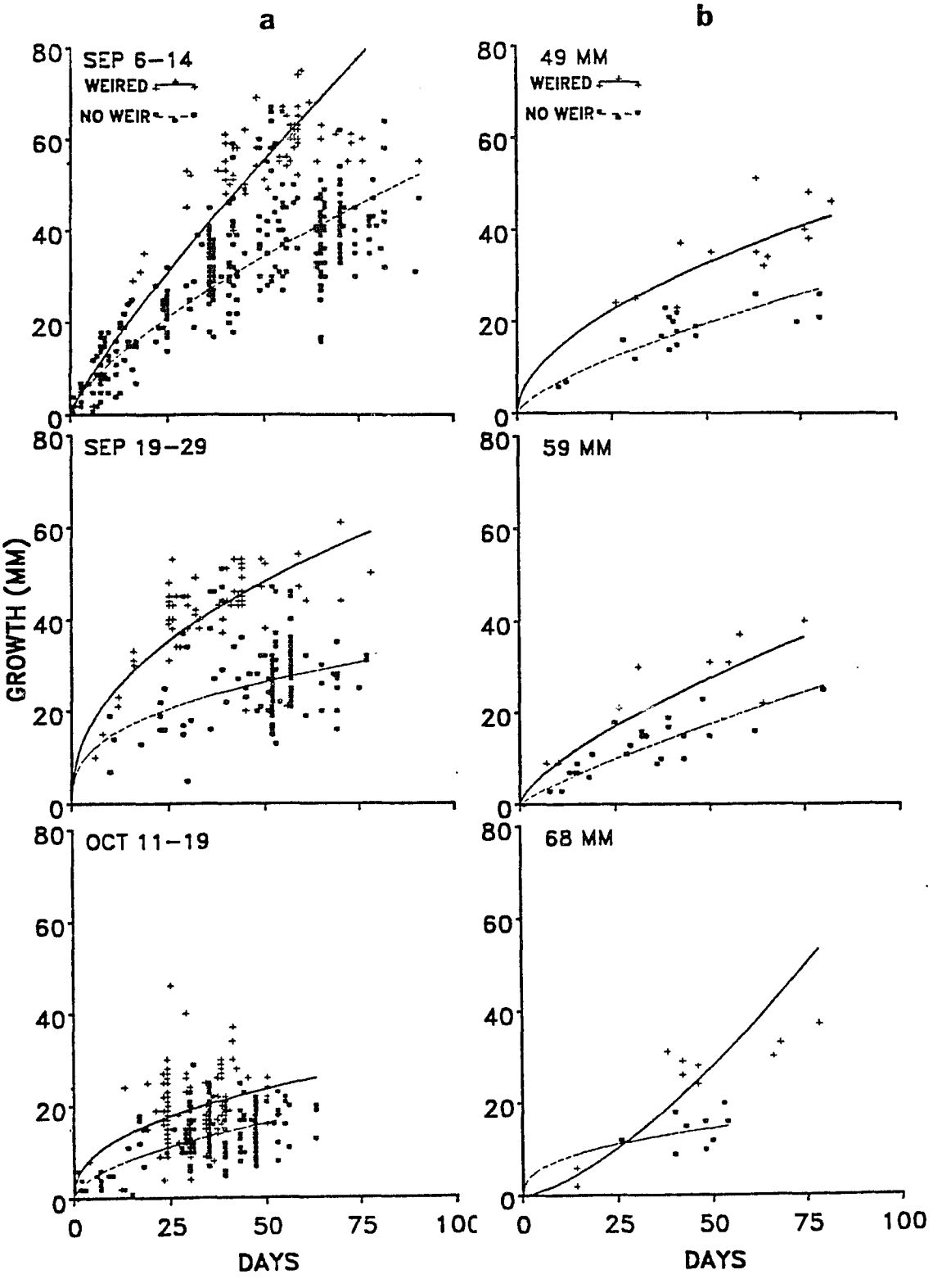


Figure 7. Exponential growth curves of white shrimp emigrating from the study ponds in a) 1983 and b) 1984. Days equals days since release. (See text for explanation of release pattern.)

and found significant differences in shrimp growth between ponds with and without weirs (Table 5). For the separate linearized exponential analysis of covariance model, pond represents the parameter for separate angles to the regression lines, ln(days) represents curvature of the lines together, and ln(days)*pond represents a parameter for different curvatures of the two lines (Table 5). Thus, shrimp grew significantly faster in the weired pond for all three release times; the curvature was significantly different for the September 6-14 release group only (Table 5, Figure 7). Growth rates slowed as the fall progressed because release time and its interactions were significant in the full model (Table 5, Figure 7).

Release size resulted in significantly different curvatures in the 1984 full model (Table 5). Furthermore, the interaction of those curvatures between release size and pond type (Ln(days)*pond*relsize) approached significance (Table 5). Although release size was significant, it is difficult to conclude from Figure 7 which release size grew faster than another. However, from analysis of variance on direct observations of growth rates in 1984, with pond types combined, both 49- and 59-mm shrimp grew significantly faster than 68-mm shrimp. When pond types were separated, there were no significant differences in growth by release length in the unweired pond but 59-mm shrimp grew significantly faster than 68-mm shrimp in the weired pond (Table 6). Differences in growth rate for different sized shrimp were not as obvious for white shrimp as they were for brown shrimp (Chapter III). Phares (1980) concluded that white shrimp growth was temperature-dependent; perhaps growth in this study was more affected by temperature than by size as temperatures decreased in the fall.

Table 6. Mean measured growth rate of white shrimp released simultaneously in the ponds with and without a weir in August, 1984.

	No weir			Weir			
Release length (mm)	Number	Mean growth rate (mm/day)	SD	Number	Mean growth rate (mm/day)	SD	*t* between ponds
49	19	0.43[a]	0.10	14	0.64[b,c]	0.15	4.44**
59	24	0.40[a]	0.15	11	0.69[b]	0.27	3.35**
68	9	0.33[a]	0.09	10	0.52[c]	0.18	3.05**

** Significant difference ($P < 0.01$) in growth between ponds at each release length.

[a,b,c] Different letters indicate significant ($P < 0.05$) difference in growth between release length groups within a given pond.

Because of significant interactions in the 1984 full model (Table 5), I conducted separate analyses of covariance for each release length with pond type as the treatment. Shrimp released at 49 and 59 mm grew significantly faster in the weired than the unweired pond; there was no difference in growth rate between ponds for 68-mm shrimp although they approached significance (Table 5, Figure 7). Shrimp grew significantly faster in the weired pond for all three experiments, including those released at 68 mm, based on direct observations of growth rate (Table 6).

Daily growth rates in 1983 ranged from approximately 0.3 to 1.4 mm/d in the unweired pond and from 0.4 to 2.5 mm/d in the weired pond, as estimated at 10 days after release and at the day of the last recapture from the 1983 growth curves in Figure 7. (Estimates earlier than 10 days would be artificially high because of the extremely steep slope the model generated when it forced the line through the intercept.) Estimated 1984 growth rates ranged from 0.3 to 0.6 mm/d in the unweired pond and from 0.2 to 1.5 mm/d in the weired pond (Figure 7). These estimated rates are similar to mean measured daily growth rates which ranged from 0.33 to 0.43 mm/d in the pond with no weir and from 0.52 to 0.69 mm/d in the pond with a weir in 1984 (Table 6). Rose et al. (1975) studied sub-adult white shrimp in Louisiana impoundments and found similar growth rates. My growth rate estimates were less than those by Klima (1974) who studied 98-144-mm white shrimp sub-adults in Galveston Bay. His study was similar to mine, except that he studied larger shrimp in open bay waters rather than in fringing marsh nurseries as I did. His study also ended earlier in autumn and was thus less affected by low temperature. Gaidry and White (1973)

estimated that white shrimp growth in Louisiana estuaries approximated 1.6 mm/d between June and late August. Although they worked on shrimp about the same size as mine, my period of study was shifted more toward the fall so my growth rates were probably reduced under cooler temperatures.

Emigration

In 1983, shrimp were released into the weired and unweired ponds at three different release times. There was a significant interaction between pond type and release time in the 1983 combined emigration time analysis of variance. I therefore analyzed emigration time separately for each of the three release times. Emigration occurred significantly later from the weired pond for the group released on September 6-14 but was significantly later from the unweired pond in subsequent experiments (Table 4). Emigration time between ponds in 1983 may have been biased by consistently later releases of shrimp in the pond with a weir (Table 4). Because emigration is stimulated by passage of weather fronts (Rogers and Herke 1985a; Chapter VI), groups released later would be exposed to relatively more emigration stimuli and their relative residence time would be reduced. This is reinforced by the fact that emigration occurred significantly sooner after release for shrimp released later, except for the September 19-21 release group in the unweired pond (Table 7). This phenomenon is probably due to decreasing water temperatures as the frequency and intensity of cold fronts increased (as reported for 1980-82 by Rogers and Herke 1985a) and is further evidence that environmental conditions stimulate emigration.

Table 7. Comparison of white shrimp mean days until emigration from each pond for groups released on different dates in 1983.

No weir		Weir	
Release dates	days	Release dates	days
September 6-7	43.2[a]	September 12-14	50.0[a]
September 19-21	47.4[a]	September 26-29	37.6[a]
October 11-12	34.9[a]	October 17-19	30.2[a]

[a] All groups within each pond are significantly different from each other ($P < 0.01$).

The obvious peaks in 1983 emigration occurred simultaneously in both ponds and were the most dramatic features of emigration (Figure 8). When data from all three release groups were combined and plotted with air temperature, the peaks apparently coincided with decreases in air temperature (Figure 9). This reinforces previous conclusions that passage of cold fronts stimulate white shrimp emigration (Lindner and Anderson 1956; Gaidry and White 1973; Rose et al. 1975; Rogers and Herke 1985a). Zein-Eldin and Renaud (1986) also reported, in a review of environmental effects on shrimp, that white shrimp survival was reduced at low temperatures and there have been numerous reports of shrimp kills at low temperatures.

In 1984, all shrimp were released on the same 2 days (Table 4). In the combined emigration time analysis of variance, there was no interaction of pond type and release size. Shrimp emigrated significantly sooner from the unweired than the weired pond, when all three release sizes were combined (Figure 10). When emigration time data for the pond types was combined, 49-mm shrimp stayed significantly longer in the ponds than 59-mm shrimp (Table 8, Figure 10). Shrimp emigrated in association with decreasing temperatures although the relationship was not as strong as in 1983, probably because of fewer recaptures (Figure 11).

The small differences in emigration time between ponds for 59- and 68-mm shrimp in 1984 (Table 4) may have occurred because these larger shrimp were physiologically ready to respond to emigration stimuli and did so from both ponds, whereas smaller shrimp remained in the weired pond longer because they experienced less drive to emigrate. It is

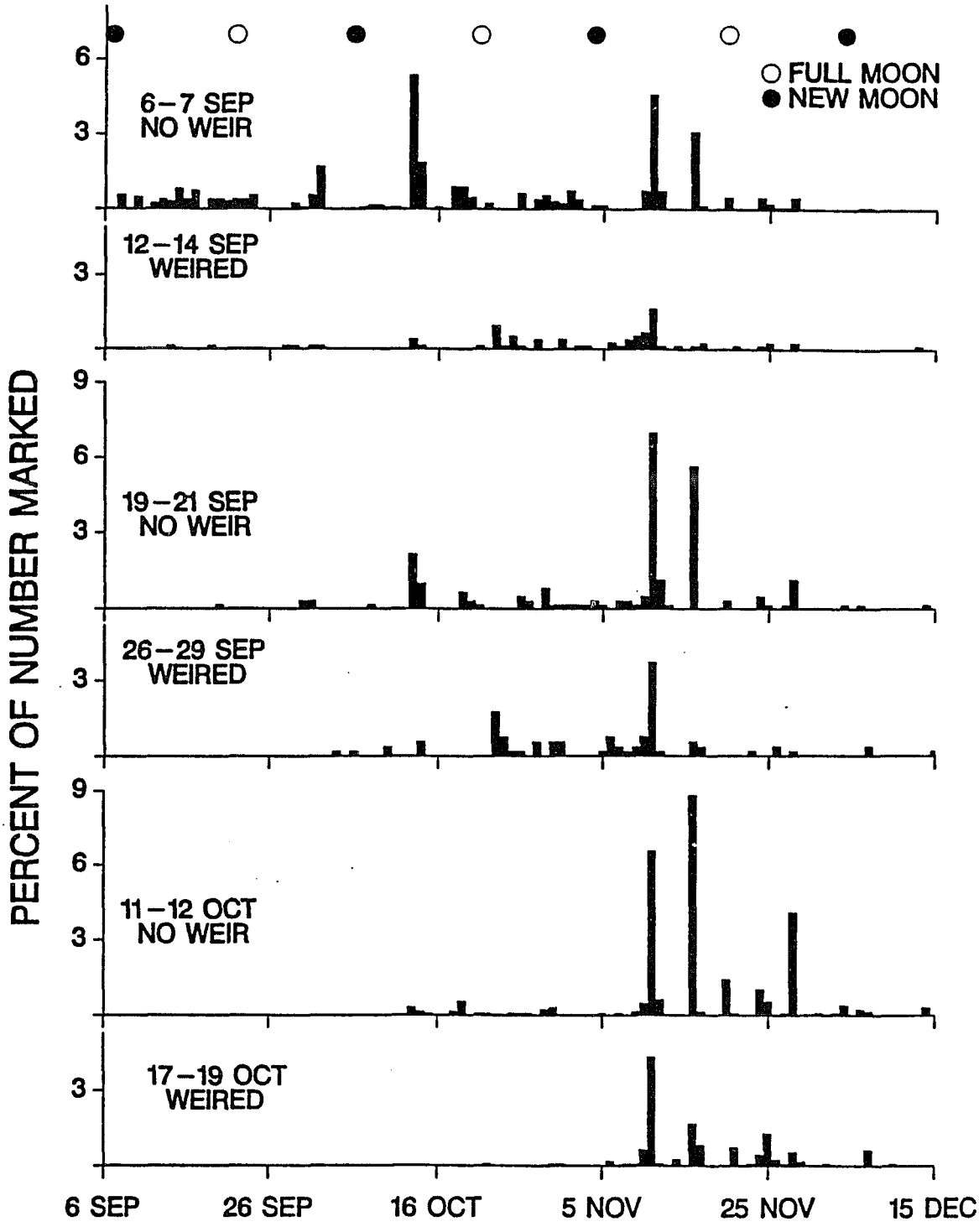


Figure 8. Emigration patterns of white shrimp released on various dates in 1983. Lunar phase is also noted.

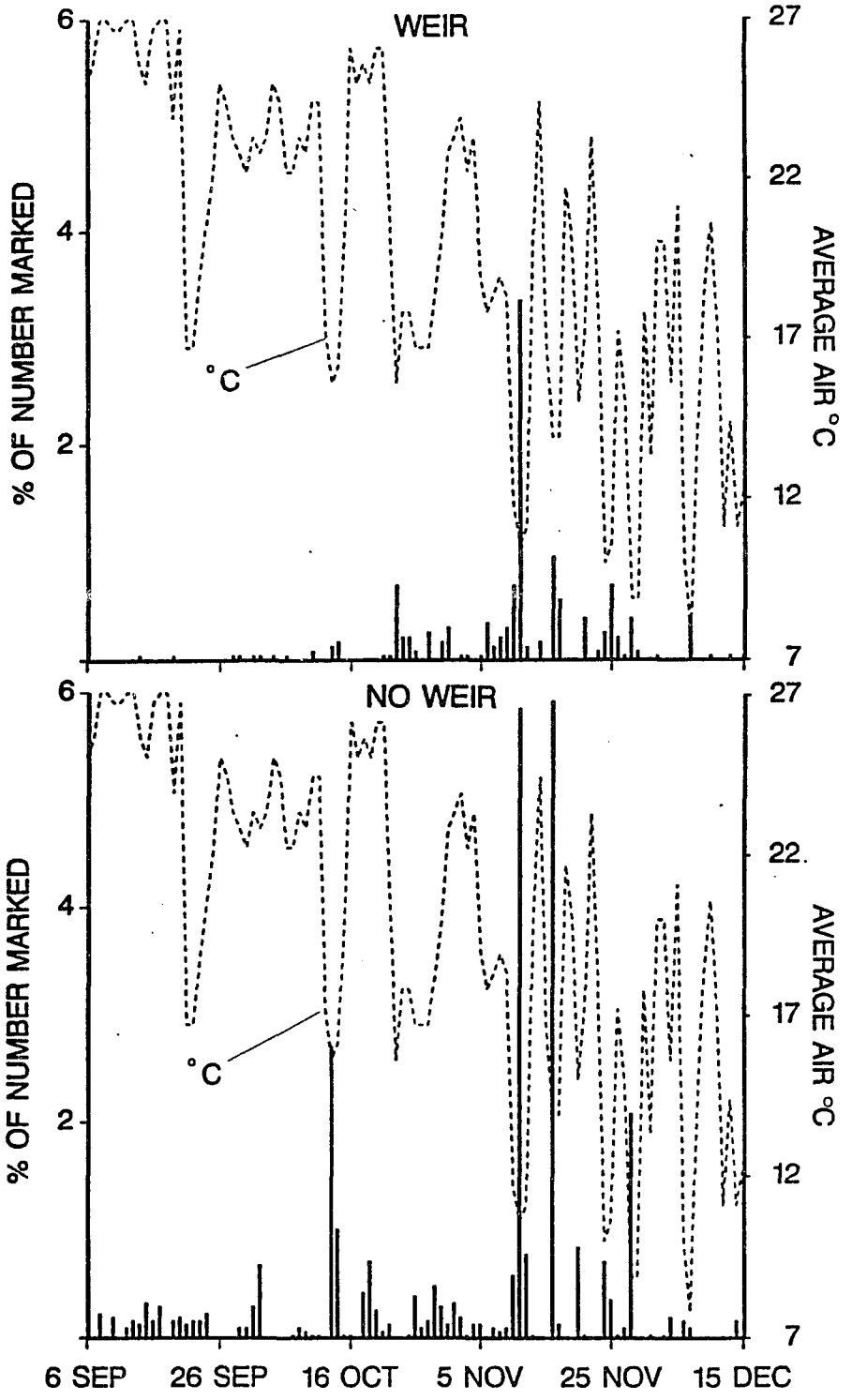


Figure 9. Relation of marked white shrimp emigration to air temperature in 1983. Recaptures from all three releases are combined.

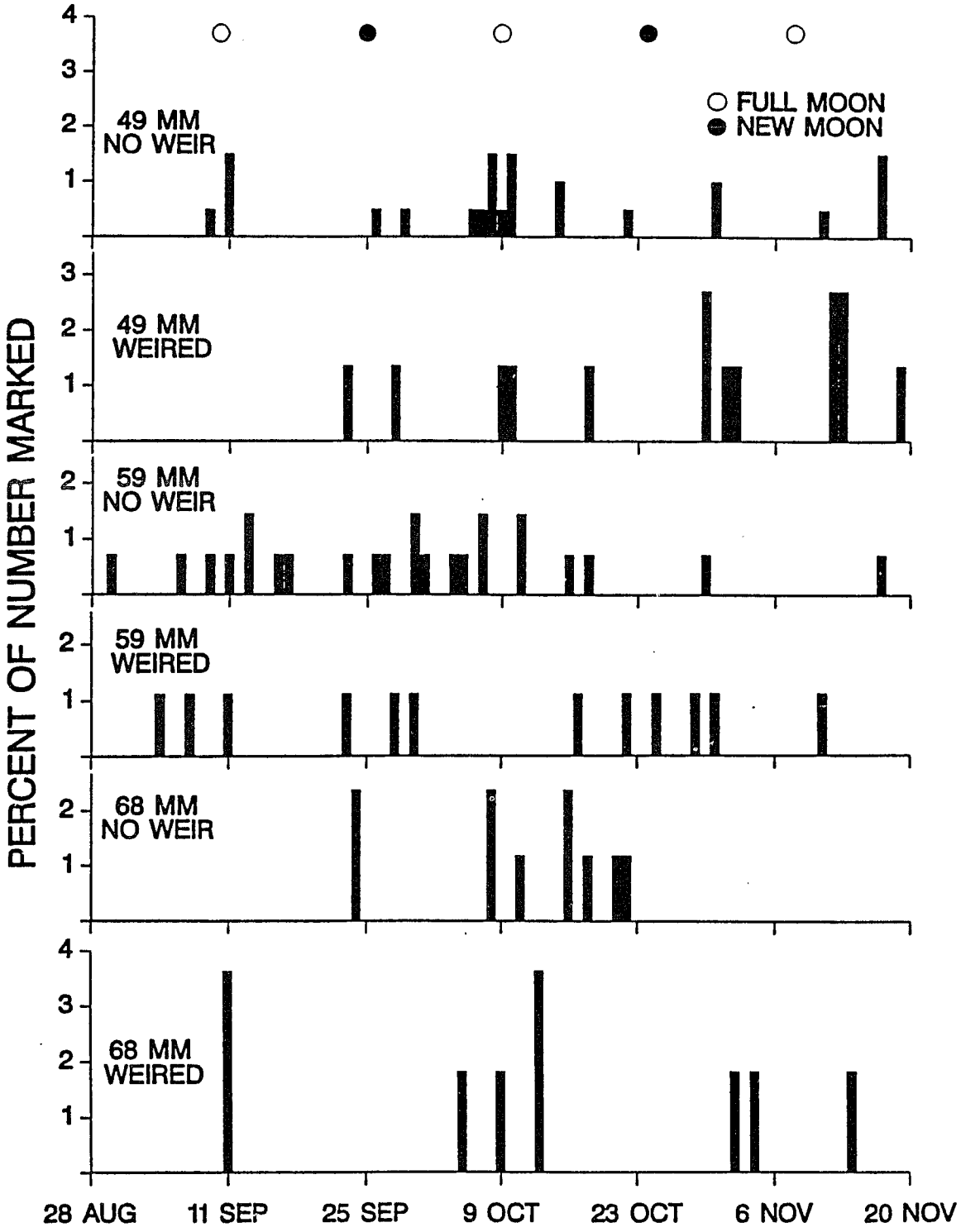


Figure 10. Emigration patterns of white shrimp released August 28-29, 1984 in the weired and unweired ponds. Lunar phase is also noted.

Table 8. Comparison of mean days until emigration for white shrimp released at various lengths but at the same time (in 1984) in each pond.

Release length (mm)	Mean days	
	No weir	Weir
49	44.1^{a}	59.9^{a}
59	31.5^{b}	40.4^{b}
68	$42.8^{a,b}$	$45.4^{a,b}$

^{a,b} Different letters in the same column indicate significant differences ($P < 0.05$).

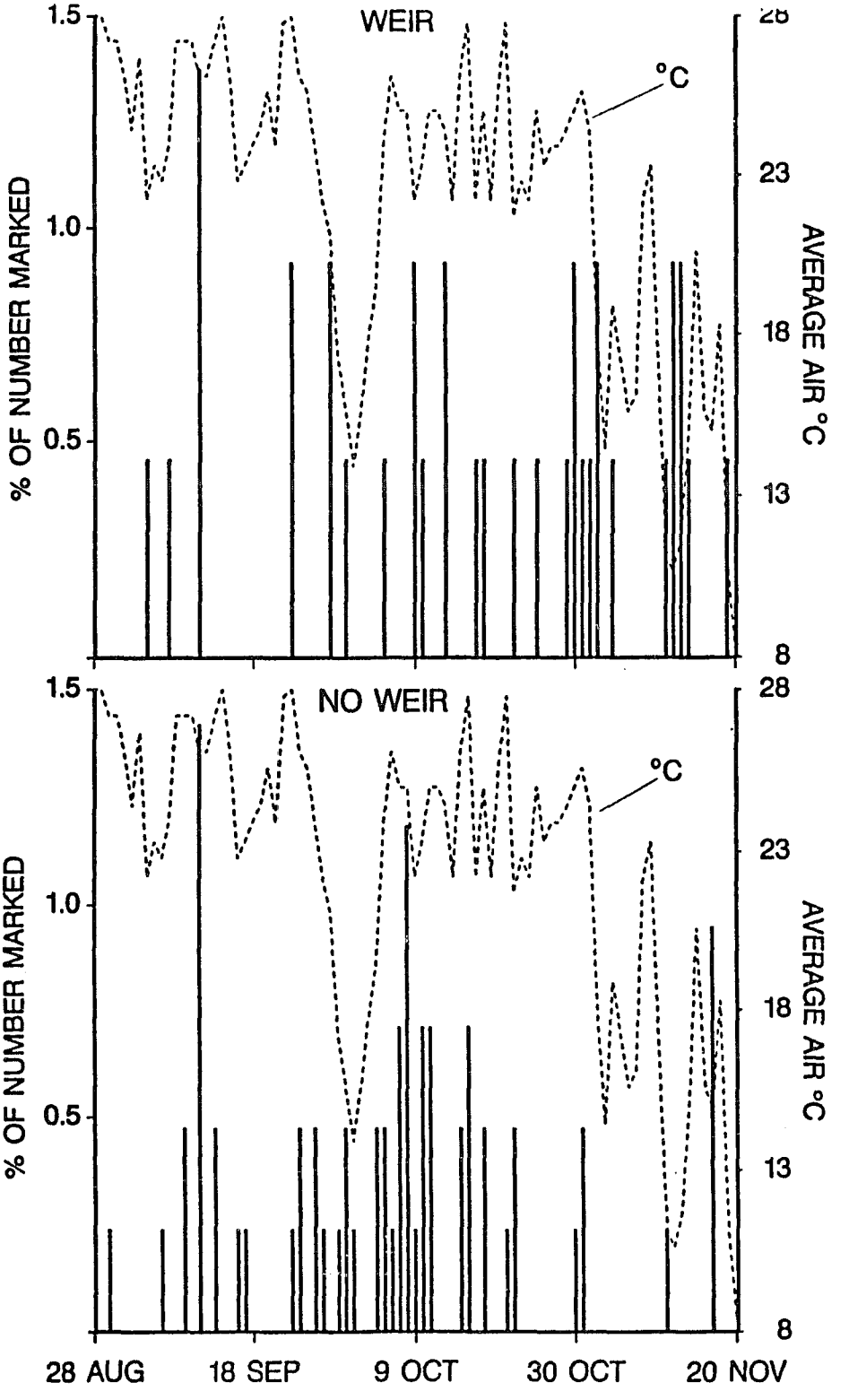


Figure 11. Marked white shrimp emigration and air temperature in 1984. Recaptures from all release sizes are combined.

also possible that, for the 59- and 68-mm release lengths, a type II error (incorrectly inferring no difference when there was one) was made due to the few recaptures (Peterman 1990).

One explanation for the trend in decreasing residence time may be that cold fronts force shrimp to emigrate from the marsh regardless of size (Figures 8-11). These tests could have suffered from low power due to few recaptures (Peterman 1990). Effects of air temperature on shrimp emigration were less obvious in 1984 perhaps because of fewer recaptures and/or less dramatic weather effects (Figure 11).

There was no apparent influence of lunar phase on white shrimp emigration (Figures 8 and 10) as was noted for brown shrimp in the previous chapter.

Discussion

There was no clear trend in white shrimp mortality in this study. As occurred for brown shrimp, mortality was greater in the east pond regardless of whether the pond was weired or not. The only known difference between the ponds was that the east pond was not as deep; perhaps this affected predation or competition for food and space.

Although not measured in this study, marsh shrimp production is likely limited in some way. As shrimp density increases, survival probably decreases due to competition for food or cover, argued by Boesch and Turner (1984) to be important factors in estuarine dependency. Juvenile white shrimp are generally thought to feed primarily on benthic meiofauna and other detritus-based organisms. Condrey et al. (1972) reported that marsh benthic meiofauna communities may be too sparse to alone support shrimp for their entire

marsh presence. It is quite possible that food competition could play an important role due to sheer numbers; in the pond without a weir an annual average of 10,871 white shrimp *survived* to emigrate from each hectare of open water (Herke et al. 1987a).

It is also possible that predation had a strong influence on mortality rates. Density of large red drum *Scieanops ocellatus*, a primary shrimp predator, was greater in the weired pond in 1983 (Herke et al. 1987b) perhaps explaining some of the greater mortality there. Density of large red drum was approximately equal in the ponds in 1984 but the density of spotted seatrout *Cynoscion nebulosus*, sand seatrout *C. arenarius*, and spot *Leiostomus xanthurus*, was greater in the pond without a weir and possibly explains the higher mortality there.

Shrimp grew faster in the weired pond in 1983 even though shrimp were released there about one week later than in the pond with no weir and were therefore more susceptible to decreasing water temperatures while at liberty than were those in the pond without a weir. Weired pond shrimp grew faster in two out of three analysis of covariance experiments in 1984. The lack of significance in analysis of covariance for the 68-mm release length group may have been due to few recaptures because direct measurements of growth revealed significantly faster growth in the weired pond.

Faster white shrimp growth in the pond with a weir apparently contributed, along with a delay in emigration, to larger shrimp emigrating from those ponds on any given day as reported by Herke et al. (1987b). The phenomenon of larger individuals in impounded and semi-impounded areas had been noted by Herke (1971, 1979), Adkins and Bowman (1976), and Perry and Joanen (1986). Whether larger shrimp size

observed in impounded areas is due to increased longevity because of reduced predation, longer residence times, or enhanced growth because of reduced competition (Boesch and Turner 1984) can now be at least partly evaluated. Greater growth rates and sometimes survival, together with longer residence at times, result in larger shrimp in ponds with weirs. The larger size at emigration (Herke et al. 1987b) from the pond with a weir did not compensate, as suggested by Perry and Joanen (1986), for the reduced total numbers of white shrimp observed emigrating from the weired than from the unweired ponds. This was true in both years because the total biomass was 79% and 65% less from the pond with the weir in 1983 and 1984, respectively (Herke et al. 1987a). It is possible there could be a minor compensation to the fishery due to a slightly lower mortality of larger shrimp subsequent to emigration and prior to entering the fishery, although mortality data for shrimp released simultaneously but at different sizes did not indicate any size-differentiated mortality. I also doubt the period of migration from the marsh to the fishery is lengthy enough to provide any noticeable difference in survival because shrimp likely migrate downstream quickly, at least as indicated to be true for brown shrimp by Knudsen et al. (1985).

Residence time was longer in the weired pond than in the unweired pond in one out of three experiments in 1983 and in all three 1984 experiments. In 1983, shrimp in all experiments were released into the weired pond a week later than the unweired pond; because emigration is likely associated with the onset of autumn weather, emigration time comparisons would have been biased in favor of the unweired pond.

There was strong evidence for a delay in emigration from the weired pond for brown shrimp in the same study ponds (see Chapter III). The dramatic influence of cold fronts on white shrimp emigration may tend obscure the influence of the weir on emigration (see Chapter VI). Emigrations of marked shrimp tended to occur in conjunction with temperature decreases regardless of the weir (Figures 9 and 11).

White shrimp emigration is clearly stimulated by passage of cold fronts. In 1983, mortality rates increased as fall progressed. To minimize mortality, water control structures should be designed and operated in response to these observations; structures should be opened briefly when cold fronts are passing to enhance shrimp emigration, thereby reducing mortality (shrimp trapped in the marsh are more susceptible to death due to low temperatures).

The total number of shrimp emigrating from the ponds with weirs was less than those emigrating from ponds without weirs (Herke et al. 1987a). More shrimp should be allowed access to areas with weirs. Because growth was greater in the pond with a weir, densities somewhat less than those measured in the pond without a weir may improve total production and also produce larger shrimp than marshes without weirs. As was pointed out by Rogers and Herke (1985a), prudence in weir placement is of utmost importance and each project should be evaluated on a case-by-case basis. The loss of shrimp, and other crustaceans and fish, must be weighed against potential gains in overall marsh management. I believe that water-control structures should not be installed in the marsh unless it is demonstrated that they help to preserve marsh. To my knowledge, this has not yet been demonstrated and the opposite may in fact be true (Cowan et al. 1988). However, if

such structures must be installed, I recommend compromises in design and operation, such as that investigated by Rogers et al. (1987), whereby fisheries losses due to structure placement are reduced.

My results indicate that marsh nursery carrying capacity for shrimp may be limited, yet growth and survival may be better at densities somewhat lower than naturally occurring maximums. It is possible that shrimp production in areas influenced by existing control structures could be maximized by first ascertaining optimum densities and then managing water control structures to allow those densities.

Conclusions

1. Instantaneous monthly natural mortality ranged from 0.86 to 2.08 in the pond with a weir and from 0.76 to 1.72 in the pond with no weir.
2. Monthly mortality was much higher than previously published for commercial-sized Gulf of Mexico white shrimp.
3. Mortality was apparently greater in the pond with the weir in 1983 but was consistently greater in the pond without a weir in 1984; thus no conclusion could be made regarding the effect of a weir on white shrimp mortality.
4. There was no apparent effect of size on observed white shrimp mortality rates.
5. Daily 1983 growth rates estimated from growth models ranged from approximately 0.3 to 1.4 mm/d in the pond with no weir and from about 0.4 to 2.5 mm/d in the pond with a weir. Both linearly estimated and directly observed daily growth rates ranged from 0.3 to 0.6 mm/d in the pond with no weir and from

0.2 to 1.5 mm/d in the pond with a weir in 1984.

6. White shrimp usually grew faster in the pond with the weir.
7. Growth rate declined with later release times in 1983.
8. There was a significant decline in growth rate for shrimp released at larger sizes in 1984.
9. There was a tendency for earlier-released, white shrimp to remain in the weired pond longer in 1983. As the fall progressed, however, emigration time became inconclusive. In 1984, emigration occurred significantly sooner from the unweired pond.
10. Peaks in emigration generally occurred simultaneously between ponds and between sizes although there was a decrease in residence time for groups released progressively later in the fall. Decreasing water temperature appears to become a more important stimulus to white shrimp emigration as the fall progresses.

CHAPTER V. Abundance and distribution of juvenile penaeid shrimp in weired, unweired, and natural Louisiana marsh waters.

Introduction

The Cameron-Creole studies assessed the effects of a water control structure on marsh fisheries production by continuously trapping all nekton emigrating from two similar marsh ponds, one with a weir at its exit and the other without a weir (Herke et al. 1984b; 1987a,b). While the conclusion of the studies was that penaeid shrimp and other species were significantly affected by the structures, these studies also provided essentially complete measurements of total shrimp numbers and biomass emigrating from specific marsh areas.

In a second study, Rogers et al. (1987) used the same ponds but placed a standard weir in the entrance of one pond and a vertically-slotted weir in the other; this was to determine whether a slotted weir could allow better brown shrimp emigration while maintaining some of the water control functions of a standard weir. They concluded 2.4 times as many brown shrimp (84% more biomass) emigrated from the pond behind the slotted weir than from behind the standard weir.

Given the conclusions of these two studies, questions regarding the functional nature of the observed reductions in shrimp emigration remained unanswered. Did the reduction occur because of blocked emigration by the weir, increased mortalities inside the weired ponds, or reduced immigration of postlarvae and juveniles into the weired ponds? Mark and recapture studies had indicated that daily mortality was sometimes less in the weired pond than in the unweired pond and that growth was probably somewhat faster in the weired ponds (Chapters

III and IV), mortality was thus not a probable explanation for the reduced emigration. The same workers found that brown shrimp emigration was often delayed (although white shrimp were generally not delayed) and neither species was prohibited from emigrating past the weir.

It was thus desirable to determine relative shrimp densities inside the weired and unweired ponds by comparing shrimp catches. I used four sampling techniques to do so. Results should further enhance our understanding of circumstances surrounding both the reduction in number and biomass of shrimp emigrating from behind weirs, and faster growth and lower mortality there.

The second objective of this portion of the study was to determine whether the number of shrimp trapped while emigrating from the unweired pond in the Cameron-Creole Study (Herke et al. 1987a,b) reflected the number that would emigrate from similar natural areas not influenced by experimental traps and screens. While it is understood that coastal marshes are vital to production of penaeid shrimp (Kutkuhn 1966; Gaidry and White 1973; Turner 1977; Zimmerman and Minello 1984), actual measurements of the numbers of juvenile shrimp utilizing these areas under natural conditions have only occasionally been attempted. Such assessments could potentially provide valuable information for 1) predicting losses in shrimp production due to habitat alterations or marsh loss, 2) input to stock-recruitment relations, and 3) inclusions in community ecology models.

Few workers have provided accurate assessments of actual shrimp density in coastal marshes. Populations of shrimp were estimated in a small Texas bayou using mark and recapture (Clark and Caillouet 1973;

Sullivan et al. 1985) and wild shrimp harvests from Louisiana impoundments were measured by Rose et al. (1975). Most other workers used trawls to determine abundance, and these were regarded as indices rather than population assessments (Loesch et al. 1976; Guillory et al. 1981).

I used density indices from two sampling techniques to indicate relative shrimp abundances in the unweired ponds, and nearby similar habitat unaffected by the experimental conditions (Figure 1), to determine whether populations enumerated while emigrating from the unweired pond were representative of densities expected to emigrate from unaltered marsh.

Methods

This portion of the study was conducted in and around the study area constructed for the Cameron-Creole Watershed Study (Figures 1, 2 and 3) (Herke et al. 1987b). Samples were collected by four different techniques from both inside the ponds and similar habitat outside the levees (Figure 1). Some work was conducted in Grand Bayou just outside the leveed areas and some was done in a nearby pond very similar to the leveed ponds but with no levee, weirs, screens, or traps. Catches from these similar habitats served as controls for catches from the leveed ponds.

In April, 1982, 10 months before trapping began for the Cameron-Creole study (Herke et al. 1987b), I initiated otter trawling in the marsh ponds that would eventually be weired and unweired (before they were isolated by levees for the study), and in a nearby similar

natural area (Figure 1), to serve as indices of relative abundance between the various habitats. The levees enclosing the two study ponds were constructed in the late fall, 1982. However, the levee dividing the two ponds was not closed until the trapping study was actually begun in February, 1983.

Trawl samples were collected from three stations every 2 weeks, if possible, from April, 1982 until February, 1985. One station was located in each study pond and another station was in a similar natural pond about 1.2 km upstream. Samples were collected with a 4.9-m otter trawl (16-mm bar mesh in the wings and 6-mm bar mesh in the codend) pulled by an airboat over a measured 0.4-km transect. The airboat speed was adjusted as necessary to cover the transect in about 5 minutes each time.

In 1984 a push-trawl (Herke 1969) was also used every 2 weeks to complement the catches obtained by otter trawl. Herke (1971) indicated that, while the species composition in the catches of the two gears overlapped, the otter trawl was better for demersal organisms and the push-trawl favored off-bottom species. The push-trawl was used on the same days as the otter trawl but only in the weired and unweired ponds. Each push-trawl sample consisted of two pushes at a constant speed for 5 minutes; one along shore and one in open water.

All trawl samples were processed according to the procedure described in Chapter II and by Herke et al. (1987b). Catch per sample was calculated and this statistic was then subjected, by gear and species, to a signed rank test (SAS PROC UNIVARIATE [SAS Institute, Inc. 1988b]) with habitat type as the treatment. Statistical

comparisons were restricted to the periods April 24 to September 25 and July 6 to December 13, for brown shrimp and white shrimp respectively, to eliminate many zero catch values. Catch data for the entire year was also examined graphically.

The methods of the trapping study have been described by Herke et al. (1987a,b) but will be briefly reviewed here. The traps were fished continuously from February 15, 1983 to February 13, 1984. After the weir was changed from one chute to the other, trapping continued from February 14, 1984 until February 15, 1985. The traps were emptied daily; a block screen was dropped into place while the trap was emptied. Thus all emigrating nekton too large to pass through 5.2-mm mesh were captured. The daily catches for each species for two entire years were thus determined and the sum of these observations provided actual measurements of the total shrimp emigration from each pond. These trapping studies led us to conclude that weirs seriously reduced the use of marshes behind them by penaeid shrimp (Herke et al. 1987a,b). Results from this portion of my research are intended to verify conclusions drawn in those previous studies.

During the studies described above, several independent investigations were conducted which provided additional information supporting my objectives. Some of the data has been reported, and will be cited appropriately, and some has not.

Bradshaw (1985) collected juvenile and postlarval brown shrimp weekly from the weired and unweired ponds with a beam trawl. White shrimp were also collected in 1983 but the results have not previously been presented. Bradshaw (1985) described his sampling and sample

processing procedures. Briefly, five sample stations were established in each study pond. Beam trawl samples were collected approximately once per week from February 21 to October 29, 1983 and from February 17 to 25 May, 1984. A 1-mm mesh Renfro beam trawl (Renfro 1963) was pulled by hand over 30 m to collect small shrimp. Samples were fixed in 10% formalin and taken to the lab where each species was enumerated. The resulting statistic of shrimp catch per sample was log-transformed (catch + 1) before being subjected to analysis of variance. I used the same approach to analyze Bradshaw's fall, 1983 white shrimp data as well.

I recieved information on shrimp densities from a cooperative study with the Center for Wetland Resources and the National Marine Fisheries Service. Samples of small shrimp were collected from the weired and unweired ponds and from a nearby natural area in 1984 with a drop-cylinder as described by Zimmerman and Minello (1984). The experimental design was to sample once per month, near the vegetated marsh edges and 20 m from shore, in three locations (weired pond, unweired pond, and the same nearby natural pond from which I collected otter trawl samples). Four replicates were collected in each habitat in each pond. The resulting statistic was catch per sample. Brown shrimp were sampled on 28 April, 18 May, and 15 June, 1984. A one-way ANOVA was used (SAS PROC GLM, SAS Institute 1988a) to test the hypotheses that brown shrimp densities were the same in weired and unweired ponds and in natural and unweired ponds. White shrimp were

sampled on 14 November, 1984 and the data was subjected to the same hypothesis tests.

Sampling gears and locations are summarized below.

	Paired study ponds			Natural control pond		
Gear	1982	1983	1984	1982	1983	1984
Otter trawl	X	X	X	X	X	X
Surface trawl			X			
Beam trawl	X	X				
Drop cylinder			X			X

Results

Density Differences Between Weired and Unweired Ponds

Trawl sampling.- Shrimp densities were compared between weired and unweired ponds by 1) comparing relative shrimp catches from the weired and no weir ponds before the levees were closed with catches after the levees were closed, and 2) comparing catches between the two ponds after the levees were closed.

In 1982, before the levees were closed, brown shrimp were significantly more abundant in the pond which would have no weir in 1983 than in the pond to be weired (Table 9, Figure 12). In 1983, average brown shrimp catch was greater in the weired pond than the no weir pond although the difference was not significant (Table 9, Figure 12). The average catch in 1983 was strongly influenced in the weired

Table 9. Average otter trawl catches of shrimp in the study ponds with and without weirs, and associated significances from signed rank tests, with pond as the treatment. Pond name is in parentheses.

Year	Pond	Mean catch	Significance of catch
	Brown shrimp		
1982	To have no weir in 1983 (L1)	169	.0137 *
1982	To have weir in 1983 (L2)	80	
1983	No weir (L1)	50	.5000
1983	Weir (L2)	114	
1982	To have no weir in 1984 (L2)	80	.0137 *
1982	To have weir in 1984 (L1)	169	
1984	No weir (L2)	43	.0605
1984	Weir (L1)	31	
	White shrimp		
1982	To have no weir in 1983 (L1)	75	.1494
1982	To have weir in 1983 (L2)	60	
1983	No weir (L1)	44	.0039 *
1983	Weir (L2)	5	
1982	To have no weir in 1984 (L2)	60	.1494
1982	To have weir in 1984 (L1)	75	
1984	No weir (L2)	65	.0400 *
1984	Weir (L1)	42	

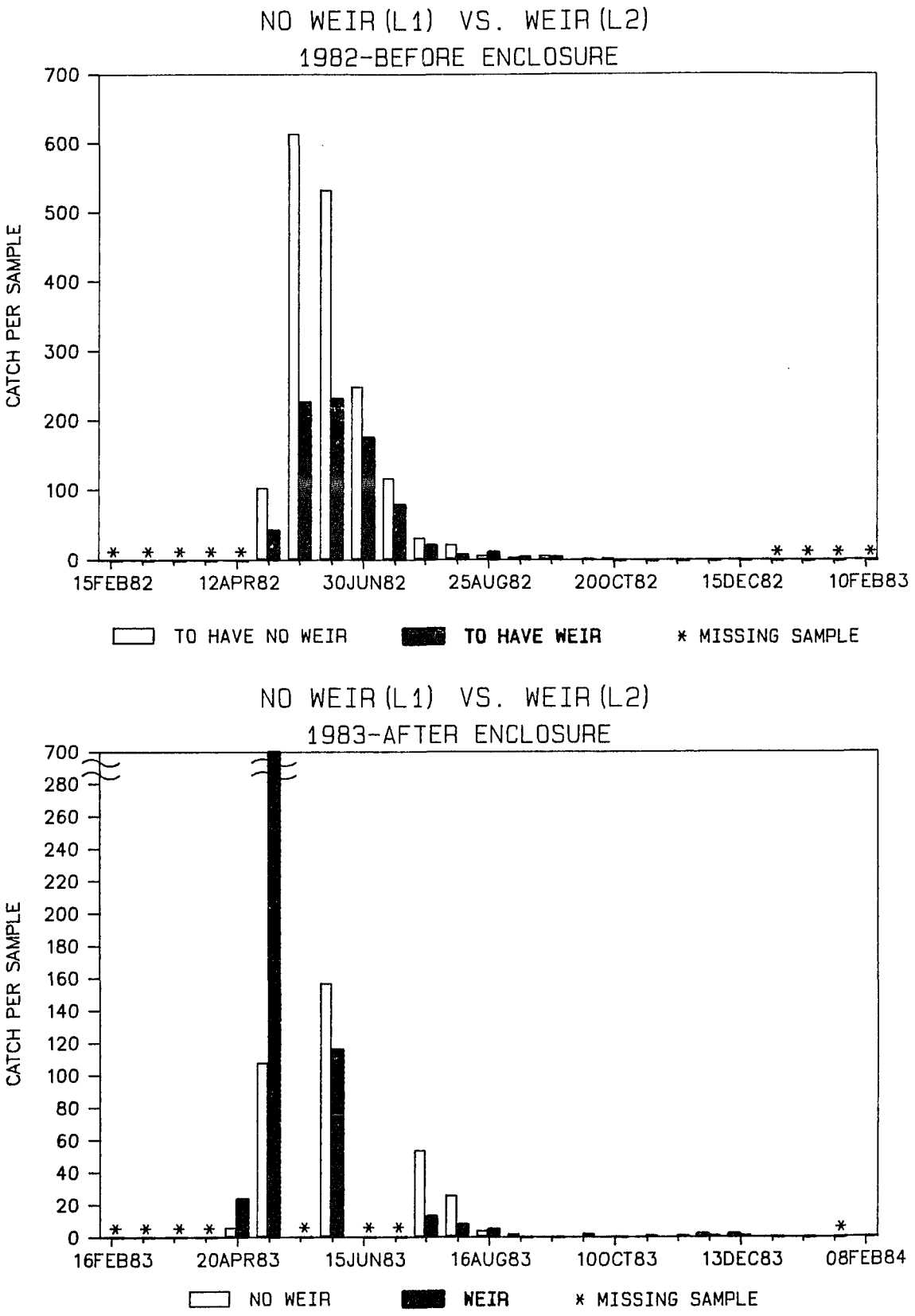


Figure 12. Relative brown shrimp catches using an otter trawl in the weired and unweired ponds before (1982) and after (1983) levee closure.

pond, however, by one extreme catch (Figure 12). The efficiency of that trawl sample was thought to have been increased by dense aquatic vegetation clogging the trawl. Brown shrimp densities may have increased for a time in the weired pond because of a delay of marked shrimp emigration from that pond (Knudsen et al. 1989).

Before the levees were closed in 1982, brown shrimp were significantly more abundant in the pond to be weired in 1984 (Table 9, Figure 13). In 1984, brown shrimp were nearly significantly less abundant in the pond with a weir than in the no weir pond (Table 9, Figure 13). Again, the single largest catch in 1984 was taken from the pond behind the weir, perhaps due to a delay in emigration (Figure 13).

Brown shrimp surface trawl catches were highly significantly greater in the pond with no weir in 1984 (Figure 14). Large catches early in the season could have resulted from high densities of shrimp or because smaller shrimp were more susceptible to the surface trawl (Figure 14).

In summary, although there were no statistically supported trends in otter trawl catches, there are strong indications the weir may have reduced trawl catches (i.e., density) of brown shrimp. This is reinforced by the beam trawling results described below.

White shrimp were significantly more abundant in the pond with no weir than in the weired pond in both 1983 and 1984 (Table 9, Figures 15 and 16). The ponds had similar densities of white shrimp in 1982 before the levees were closed (Table 9, Figures 15 and 16). White

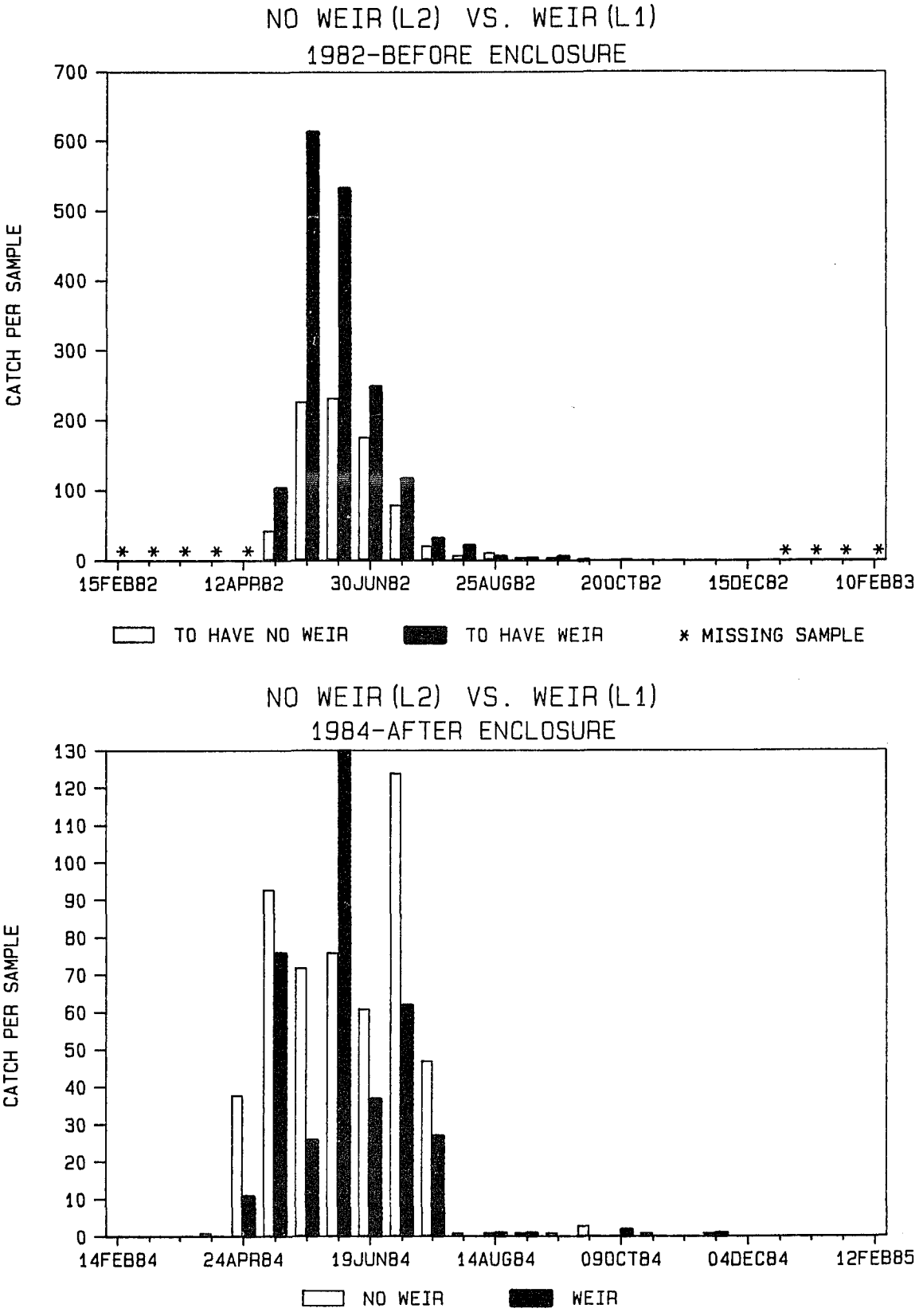


Figure 13. Relative brown shrimp catches using an otter trawl in the weired and unweired ponds before (1982) and after (1984) levee closure.

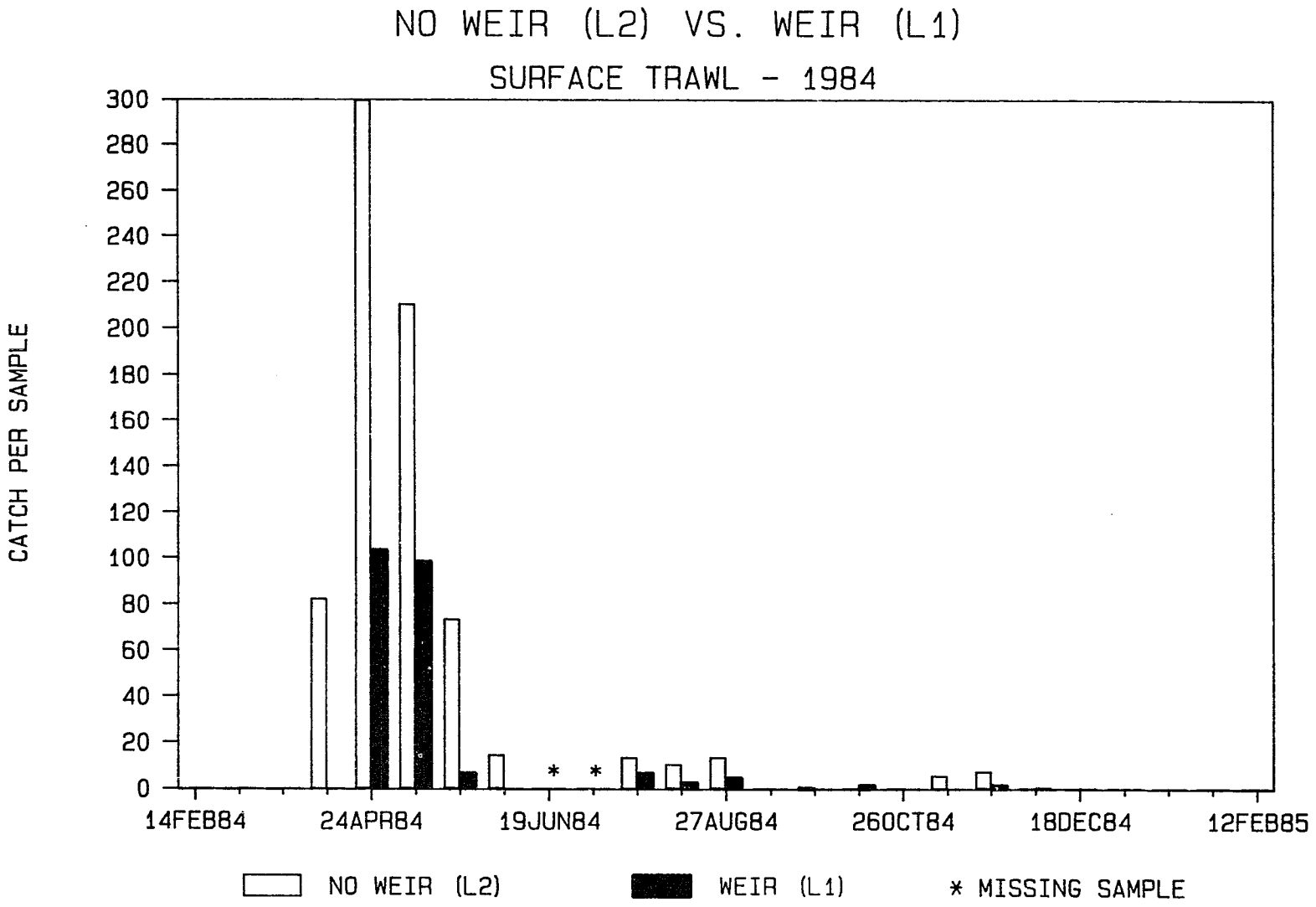
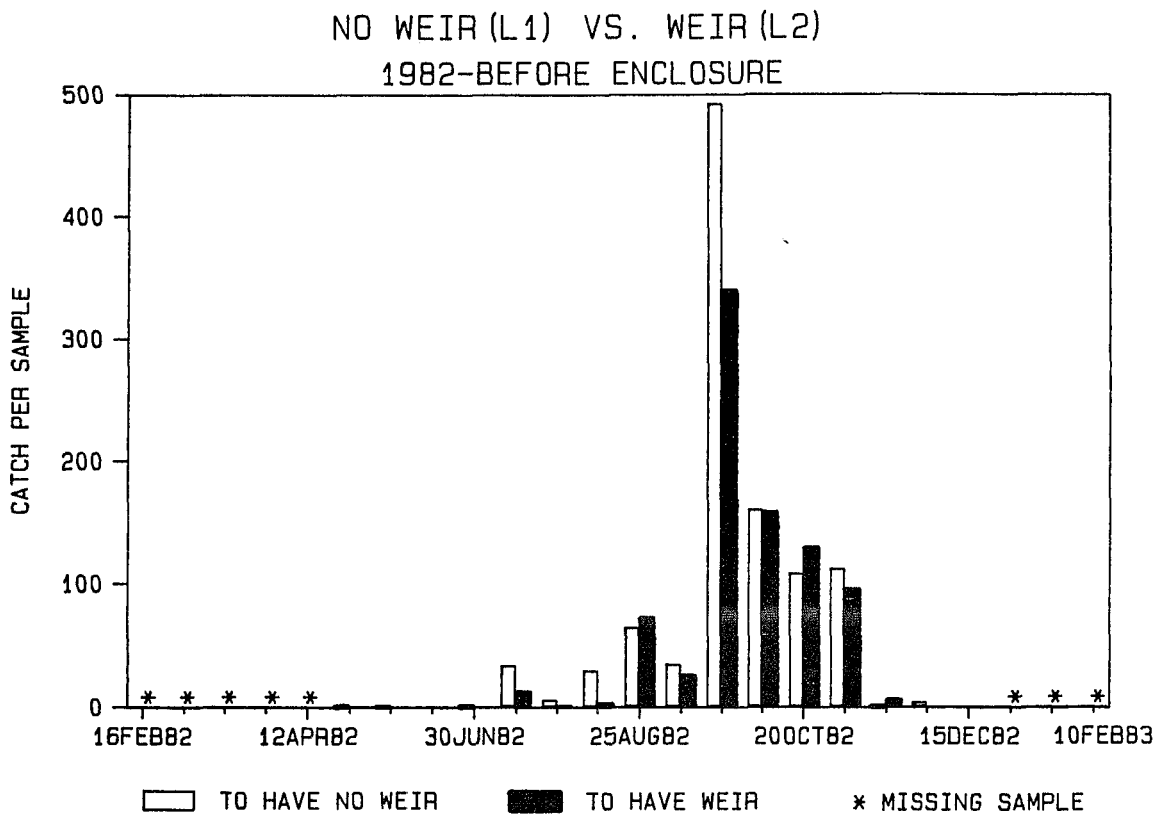


Figure 14. Relative 1984 brown shrimp catches using a surface trawl in the weired and unweired ponds.



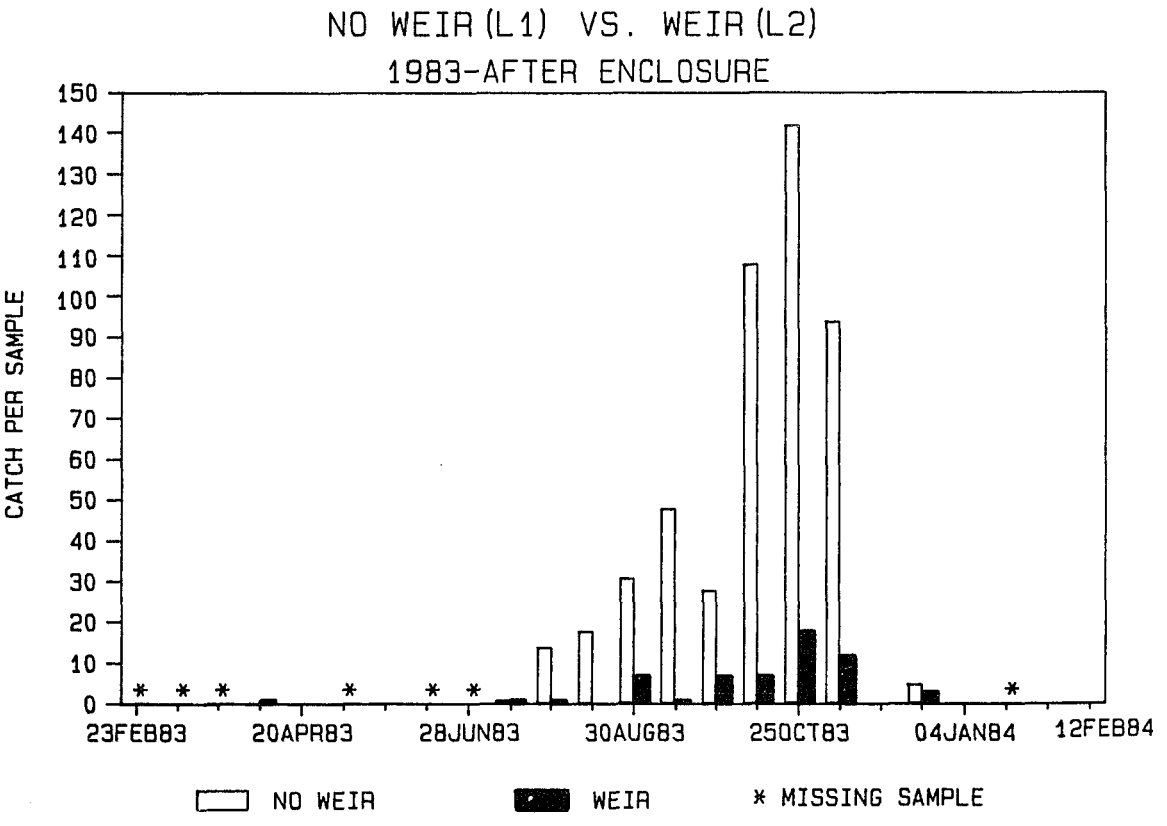


Figure 15. Relative white shrimp catches using an otter trawl in the weired and unweired ponds before (1982) and after (1983) levee closure.

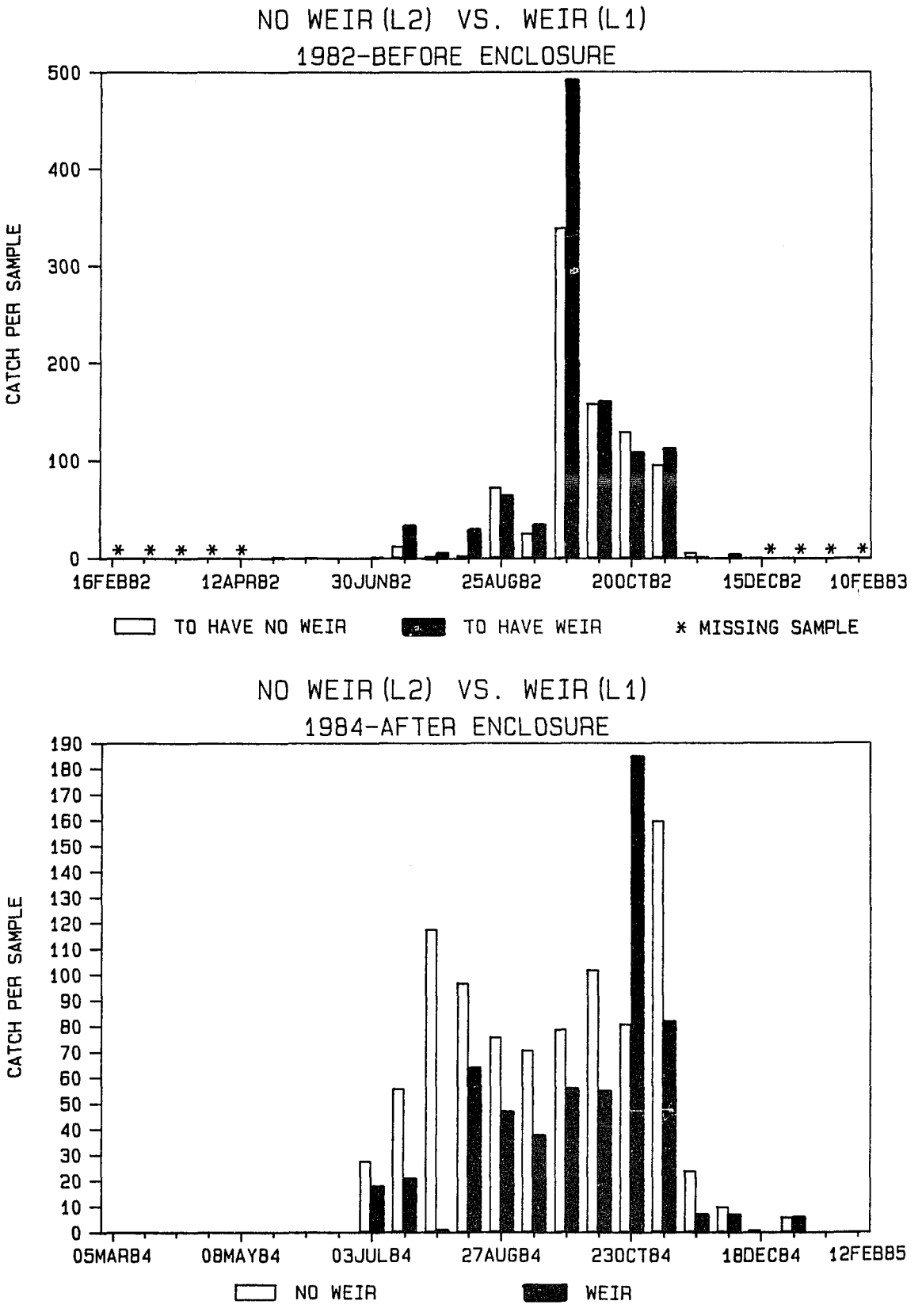


Figure 16. Relative white shrimp catches using an otter trawl in the weired and unweired ponds before (1982) and after (1984) levee closure.

shrimp surface trawl catches were significantly greater in the pond with no weir in 1984 (Figure 17). Clearly, the weir had a dramatic influence on the abundance of white shrimp behind it.

Beam Trawl Sampling.- Bradshaw (1985) concluded that postlarval and juvenile brown shrimp abundance was reduced behind the weirs in both 1983 and 1984 (Table 10). I analyzed Bradshaw's unpublished white shrimp data and found that catches of postlarval and juvenile white shrimp were significantly greater in the unweired pond in 1983 (Figure 18, Table 10).

Drop-cylinder Sampling.- When sampled 1 m from the marsh grass edge, brown shrimp were significantly more abundant in the no weir pond than in the weired pond (Figure 19). The average brown shrimp density 20 m from the marsh edge was greater in the no weir pond but not significantly so (Figure 19). Shrimp were absent in the 20 m sample on 15 June but were dramatically more dense in the 1 m sample that day (Figure 19). The shift closer to the grass on that day could help explain the lack of significance in the 20 m samples. Densities of juvenile white shrimp 1 m from the edge were greater in the unweired pond than the weired pond but the differences were not significant (Figure 20). White shrimp densities were not significantly different 20 m from the edge (Figure 20).

To summarize, the pond having the greater average catch (from Table 9) is shown below, by gear and year.

	Before enclosure		After enclosure	
Year	Pond with more	Significant?	Pond with more	Significant?
Brown shrimp - otter trawl				
1	111% more in no weir	Yes	128% more in weired	No
2	111% more in weired	Yes	39% more in no weir	No
Brown shrimp - surface trawl				
2			273% more in no weir	Yes
Brown shrimp - beam trawl				
1			33% more in no weir	Yes
2			435% more in no weir	Yes
Brown shrimp - drop cylinder				
2			278% more in no weir	Yes
White shrimp - otter trawl				
1	25% more in no weir	No	780% more in no weir	Yes
2	25% more in weired	No	55% more in no weir	Yes
White shrimp - surface trawl				
2			750% more in no weir	Yes
White shrimp - beam trawl				
1			762% more in no weir	Yes
White shrimp - drop cylinder				
2			600% more in no weir	No

Otter trawl catches of brown shrimp were greater in the weired pond in 1983 but not 1984, relative to the background densities in 1982. All other measures of brown shrimp density were greater in the unweired

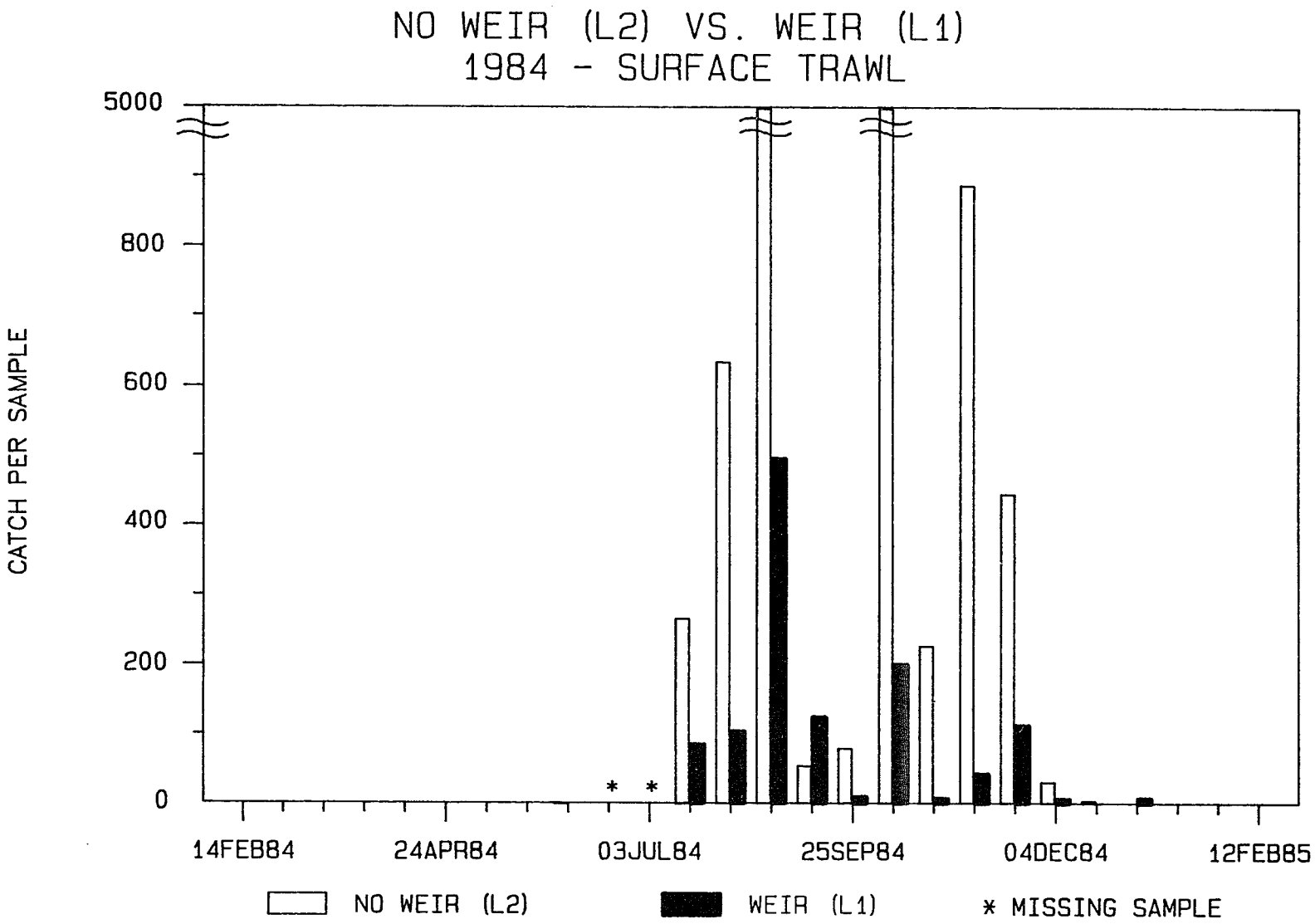


Figure 17. Relative 1984 white shrimp catches using a surface trawl in the weired and unweired ponds.

Table 10. Total beam trawl catches of brown and white shrimp from weired and unweired ponds in 1983 and 1984 (partly from Bradshaw 1986).

Year	Weired	Unweired
	Brown shrimp	
1983	783	1040[a]
1984	144	771[a]
	White shrimp	
1983	120	1034[b]

[a] $P < 0.10$

[b] $P < 0.05$

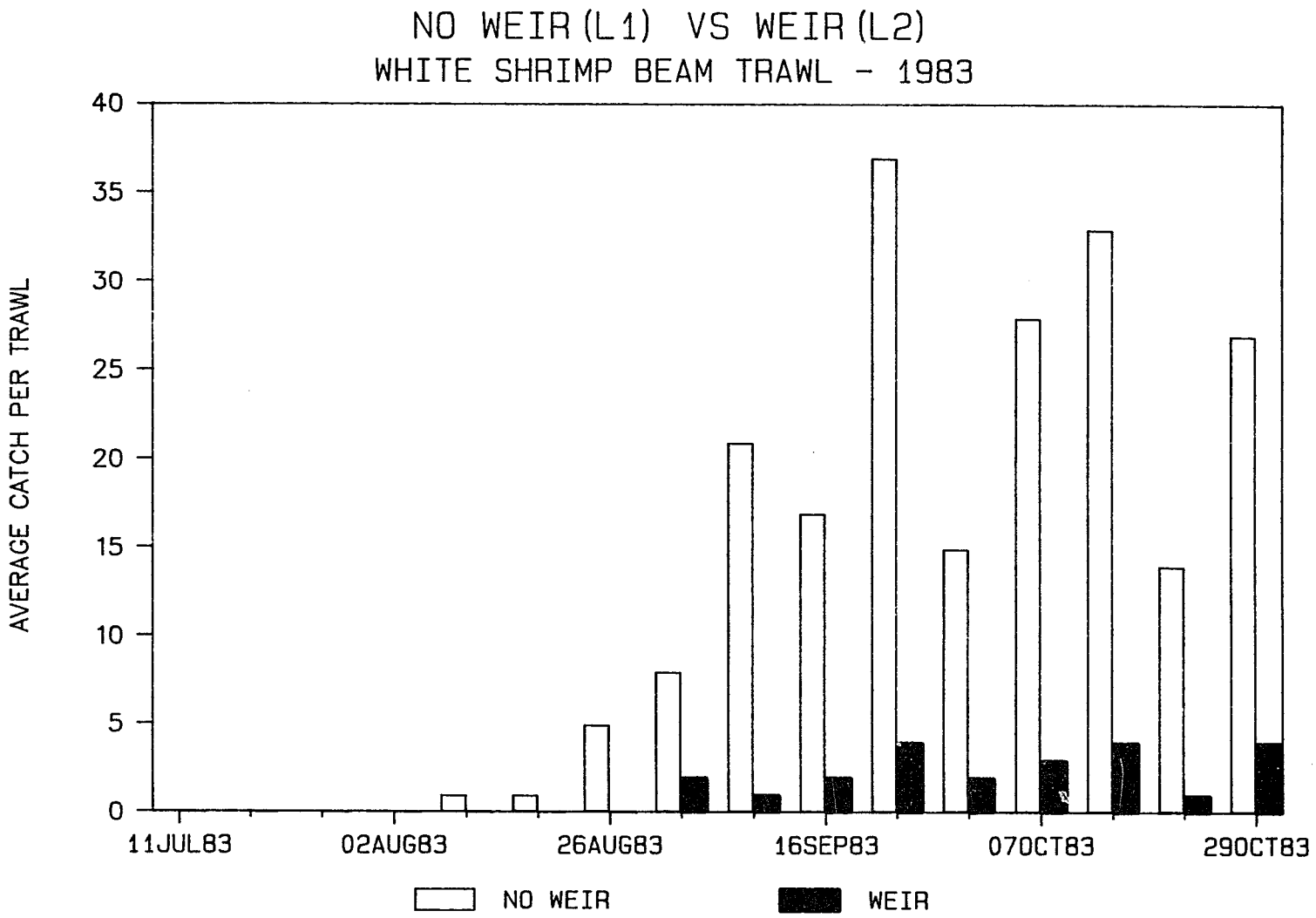


Figure 18. Relative postlarval and juvenile white shrimp catchesusing a beam trawl in the weired and unweired ponds in 1983.

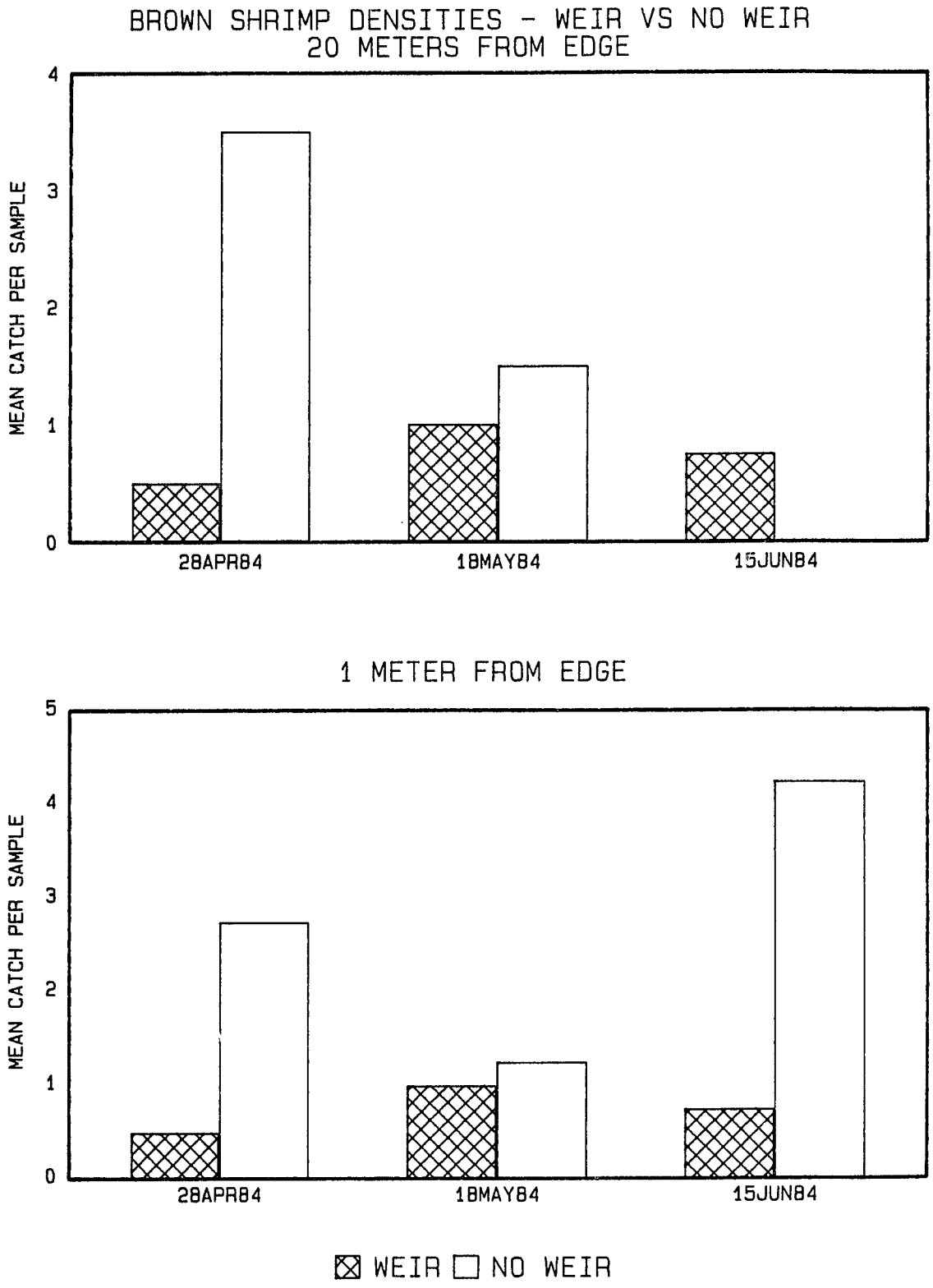


Figure 19. Relative mean densities of juvenile brown shrimp in weired and unweired ponds as measured with a drop cylinder at 1 and 20 m from the grass edge in 1984.

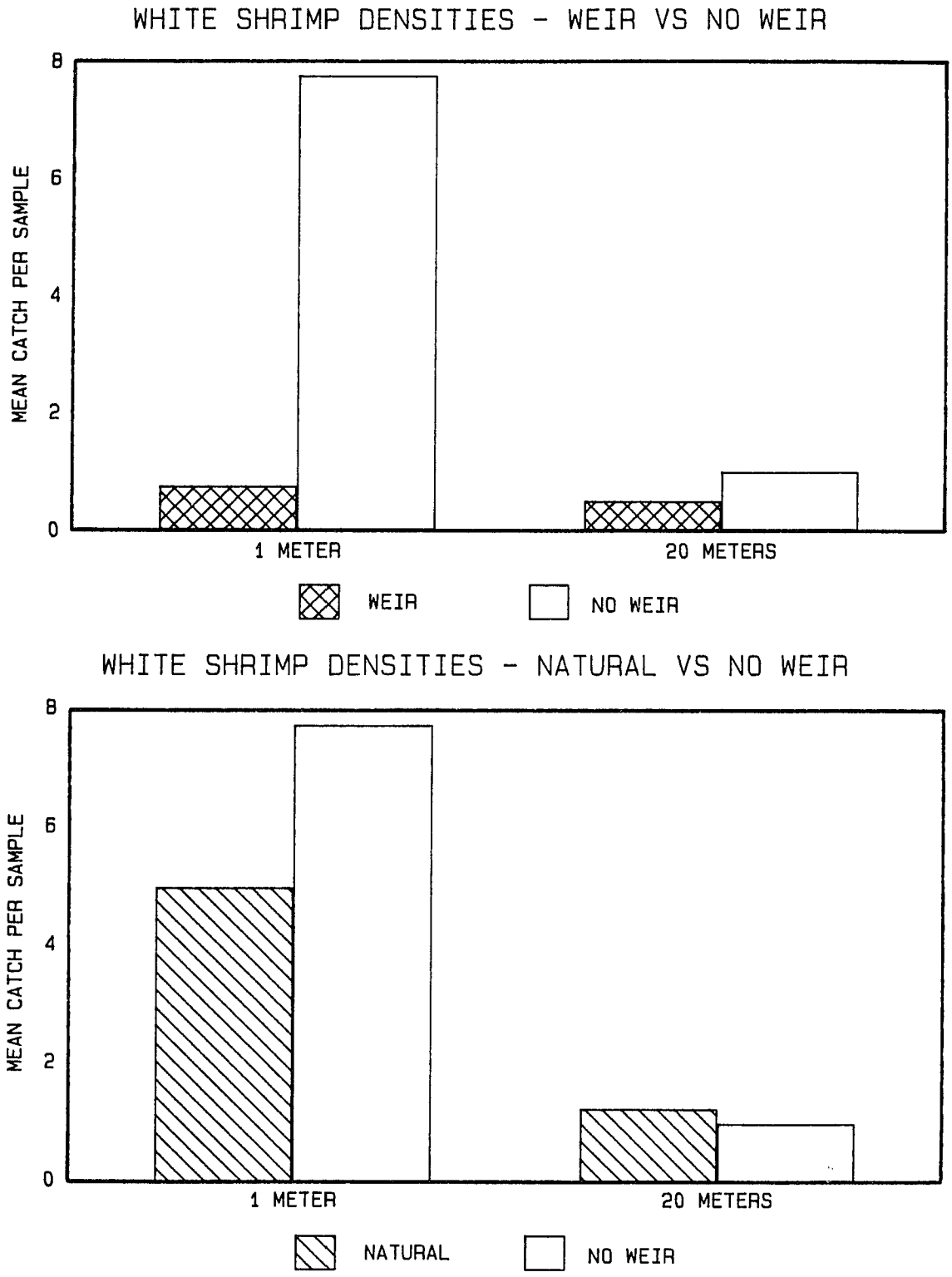


Figure 20. Mean white shrimp densities in weired, unweired, and natural ponds on November 14, 1984, as measured by drop cylinder.

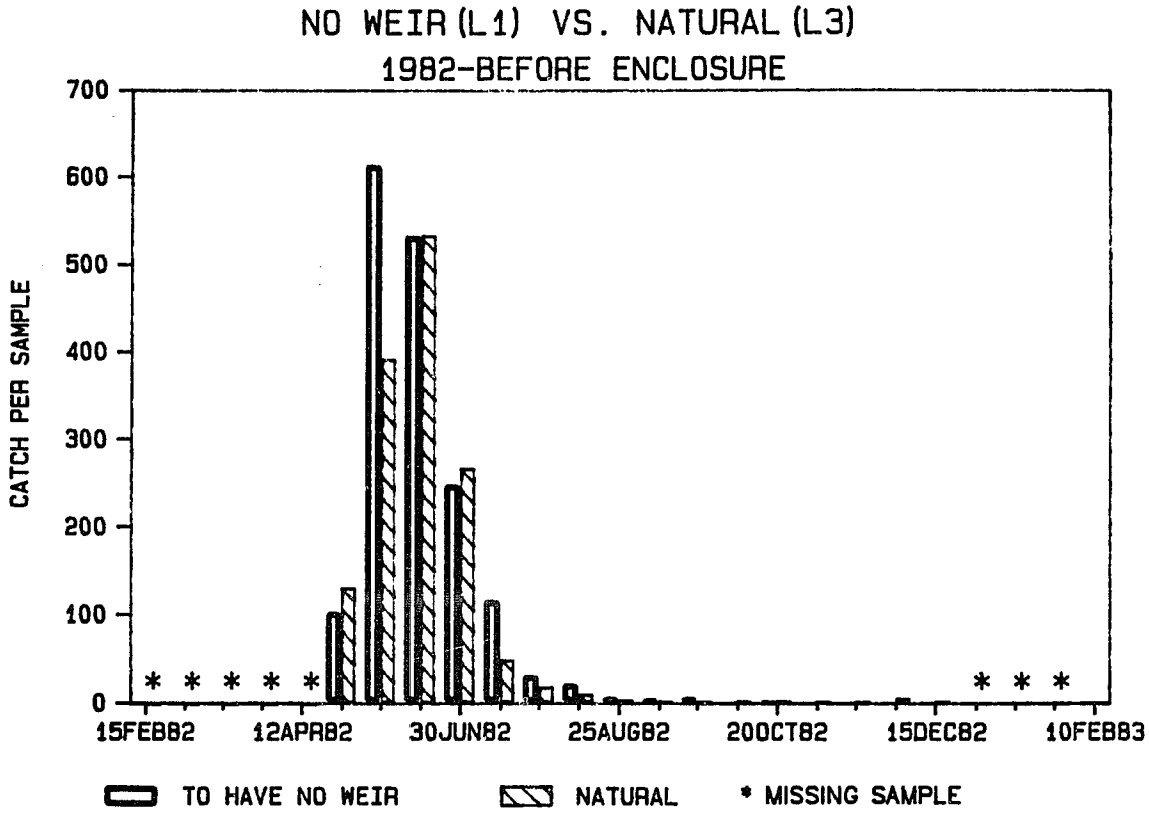
pond than the weired pond. All measures of white shrimp density were consistent with the hypothesis that there were more white shrimp in the unweired pond.

Abundance of Shrimp in Natural Marsh

Trawl sampling-. Comparisons of shrimp density between the unweired pond and the natural pond were made by 1) comparing relative catches from the unweired pond, and a nearby natural pond, before the levees were closed, and 2) comparing those results to results of a comparison between the same two ponds after the levees were closed.

Average brown shrimp catch was greater in the pond to be the 1983 unweired study pond than in the natural pond but the difference was not significant (Figure 21, Table 11). In 1983, after enclosure, catches were again greater in the unweired study pond than in the natural pond but the difference was not significant (Figure 21, Table 11). Brown shrimp catches from the natural pond in 1982 were usually greater than those in the pond to have no weir in 1984 although not significantly (Figure 22, Table 11). After enclosure in 1984, catches were significantly larger from the natural pond (Figure 22, Table 11) indicating there may have been a reduction in brown shrimp densities due to the screens and traps. These mixed results generally indicate that the experimental screens and traps in the channels leading to and from the no weir pond may have had some influence on brown shrimp densities although there is not enough clear evidence to conclude the effect was dramatic.

There was no obvious difference in 1982 white shrimp abundance between ponds prior to enclosure. Average catch was greater in the



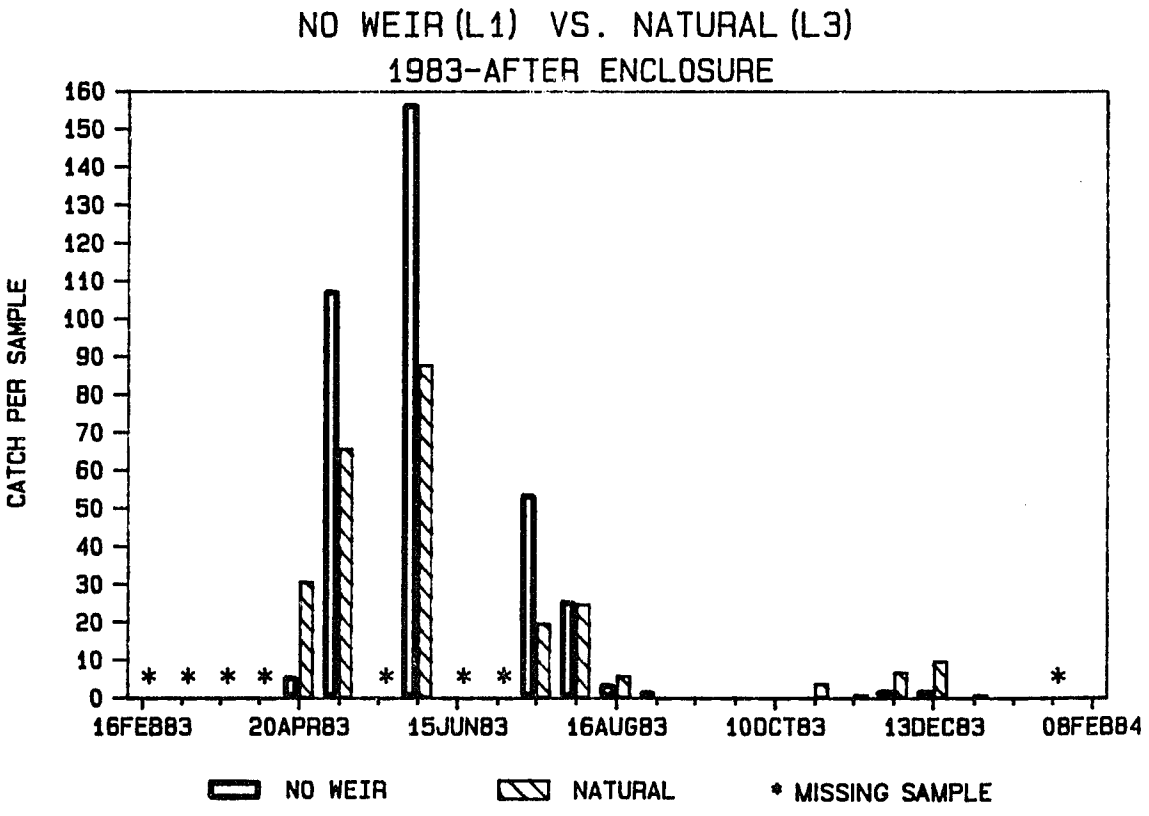
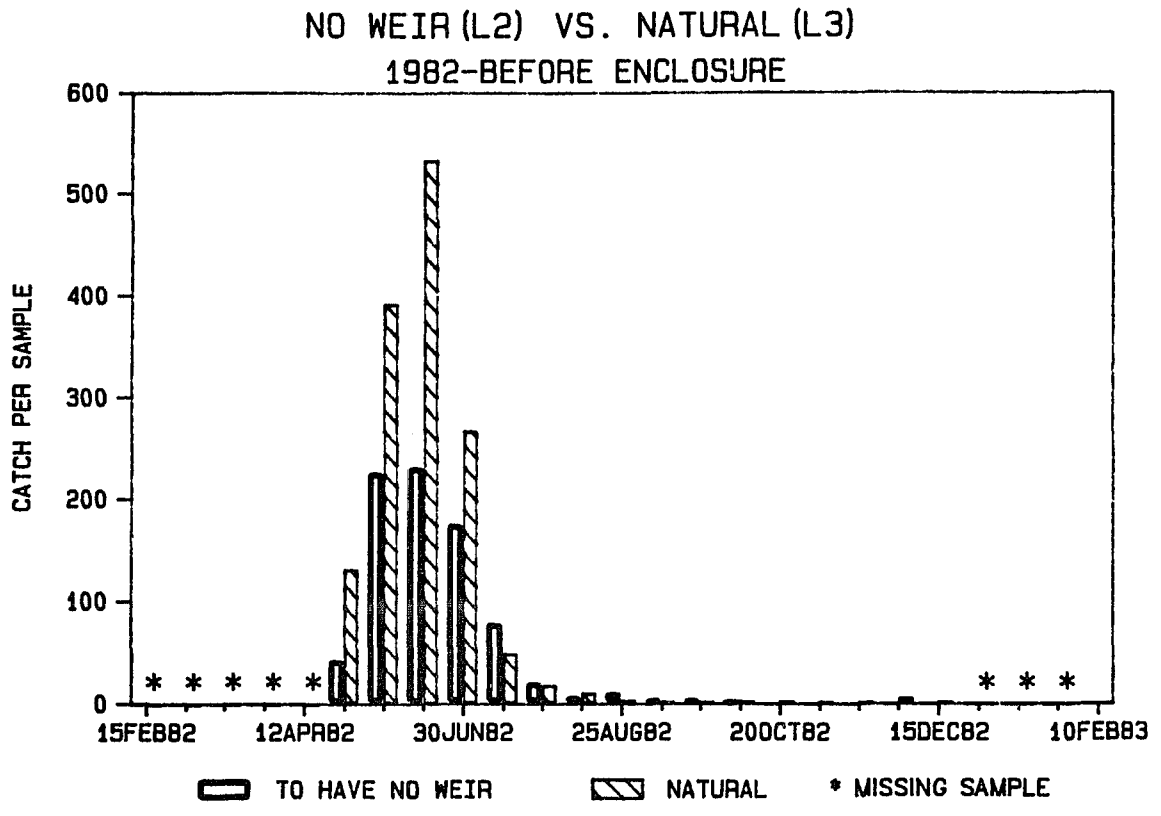


Figure 21. Relative brown shrimp catches in the natural and the unweired ponds using an otter trawl before (1982) and after (1983) levee closure.

Table 11. Average otter trawl catches of shrimp in the ponds having no weir in 1983 and 1984, before and after enclosure, compared to a nearby natural pond, and associated significances from signed rank tests, with pond as the treatment. Pond names are in parentheses.

Year	Pond	Mean catch	Significance of ln(catch)
	Brown shrimp		
1982	To have no weir in 1983 (L1)	169	.3008
1982	Natural (L3)	140	
1983	No weir (L1)	50	.1250
1983	Natural (L3)	29	
1982	To have no weir in 1984 (L2)	80	.3848
1982	Natural (L3)	140	
1984	No weir (L2)	43	.0195 *
1984	Natural (L3)	119	
	White shrimp		
1982	To have no weir in 1983 (L1)	75	.9502
1982	Natural (L3)	73	
1983	No weir (L1)	44	.7646
1983	Natural (L3)	104	
1982	To have no weir in 1984 (L2)	60	.5332
1982	Natural (L3)	73	
1984	No weir (L2)	65	.6533
1984	Natural (L3)	74	



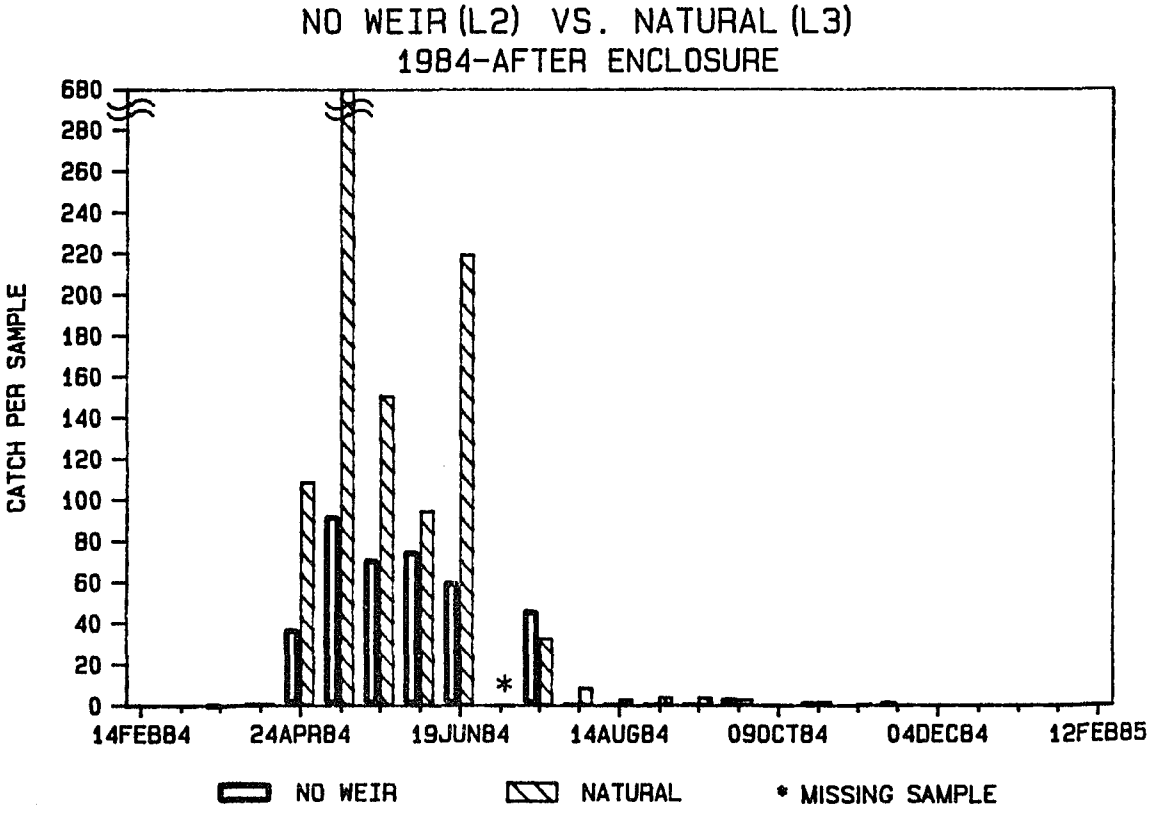
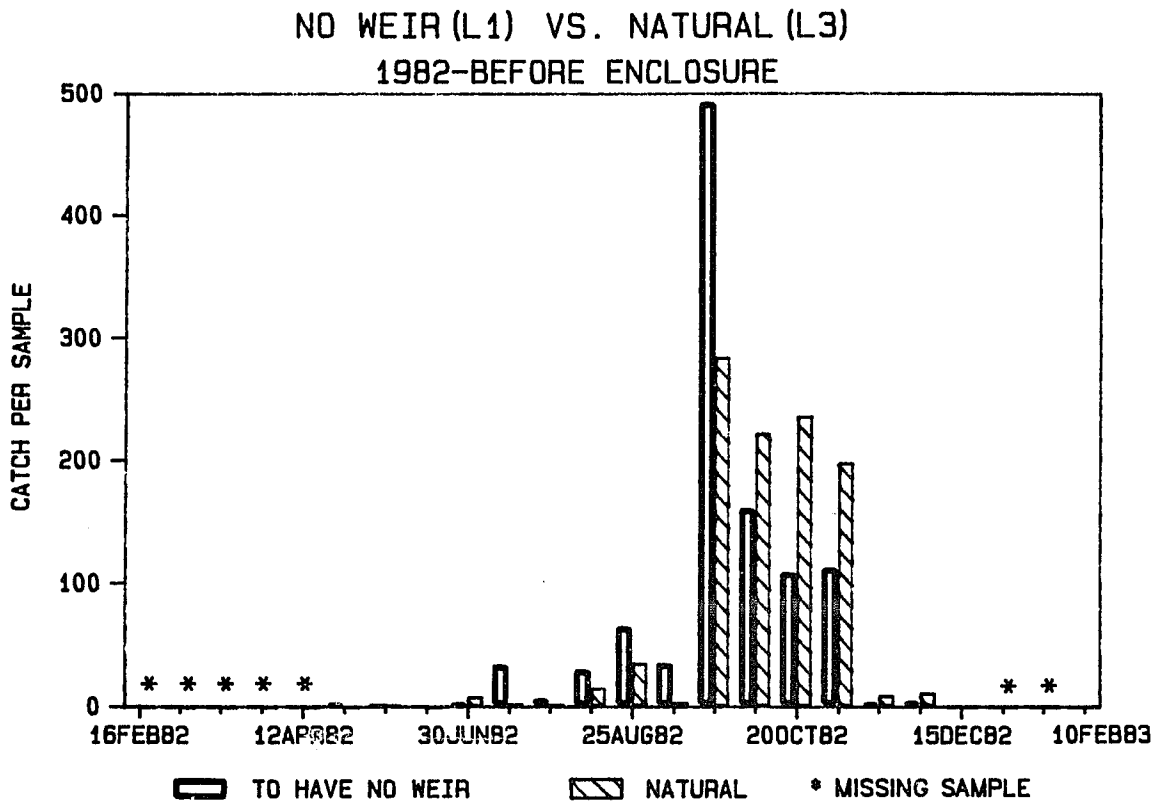


Figure 22. Relative brown shrimp catches in the natural and the unweired ponds using an otter trawl before (1982) and after (1984) levee closure.

natural pond than in the unweired pond after enclosure in 1983 although not significantly (Figure 23, Table 11). The greater average catch in the natural pond was strongly influenced in 1983 by a single, large catch. It is interesting that early in the season the relative abundance was greater in the pond having no weir, which is closer to Lake Calcasieu, while later in the season, catches in the natural pond were greater (Figure 23).

Essentially the same seasonal pattern occurred in the pond having no weir when compared to the natural pond in both 1982 and 1984 (Figure 24). The difference in mean catches between natural and no weir ponds was almost the same in 1982 and 1984 (Table 11). Thus, for the 1982/1984 otter trawl catch comparisons, it is unlikely that the traps and screens negatively affected white shrimp densities in the ponds having no weirs, but, because catches were relatively greater in the natural pond in 1983, as compared to the difference between ponds in 1982, there is a possibility that the screens and traps reduced the number of shrimp in the unweired pond.

Drop-cylinder sampling.- Brown shrimp were significantly more abundant in the natural than the unweired pond at both 1 and 20 m from the grass edge (Figure 25). There was no significant difference in white shrimp abundance between the no weir and natural ponds at either distance from the grass (Figure 20).



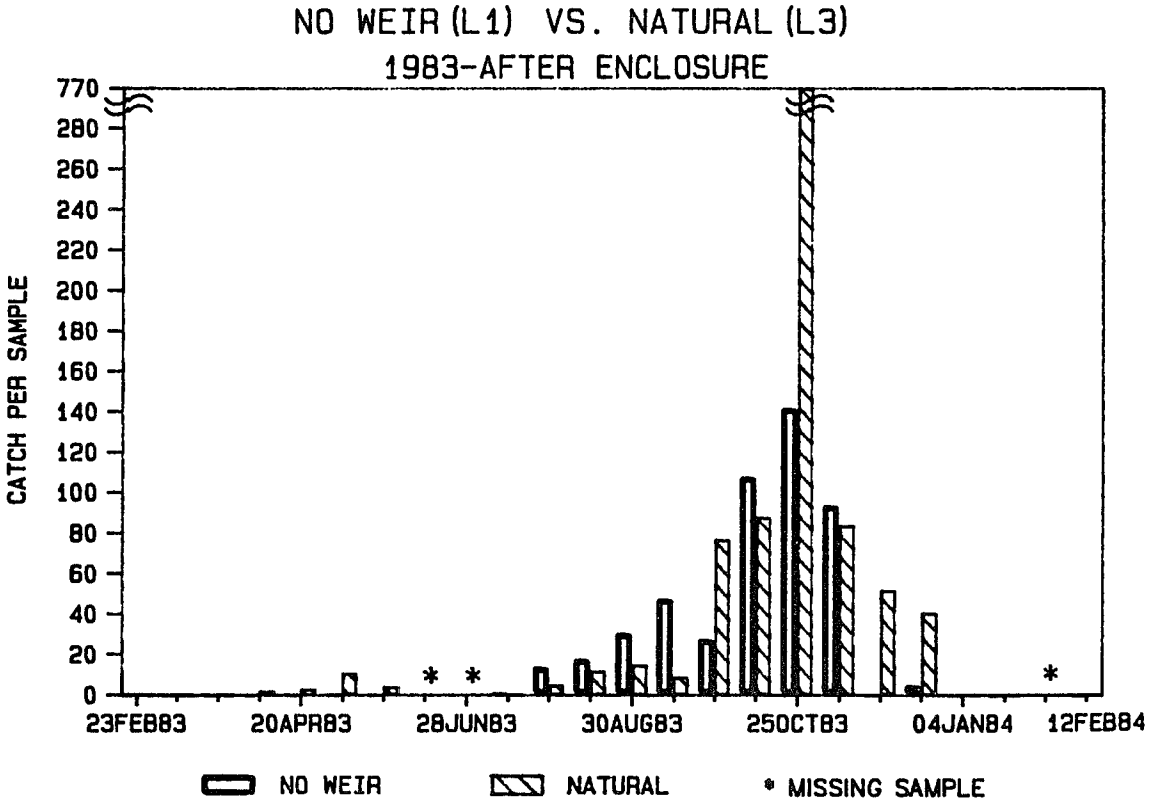


Figure 23. Relative white shrimp catches in the natural and the unweired ponds using an otter trawl before (1982) and after (1983) levee closure.

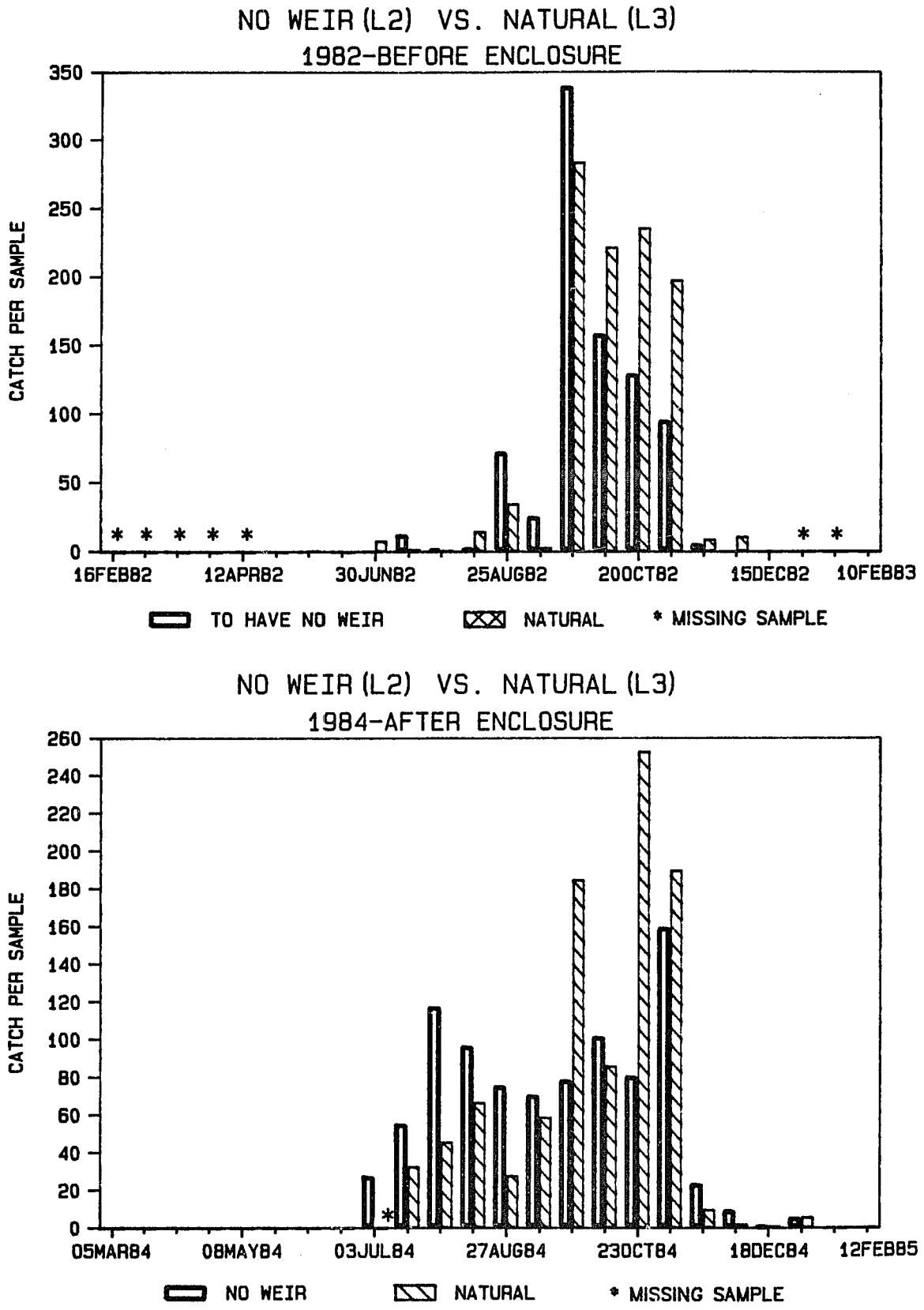


Figure 24. Relative white shrimp catches in the natural and the unweired ponds using an otter trawl before (1982) and after (1984) levee closure.

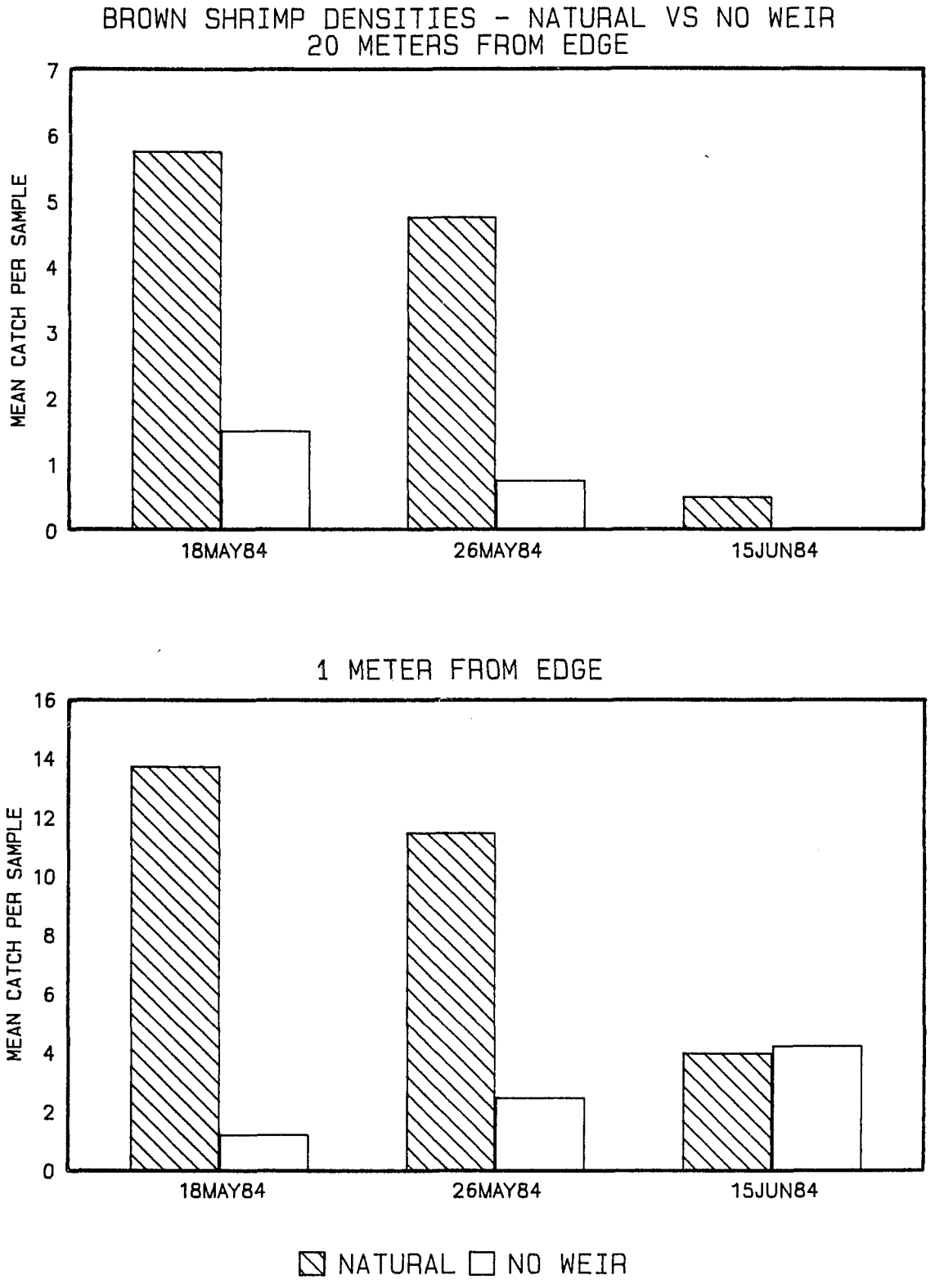


Figure 25. Relative mean densities of juvenile brown shrimp in natural and unweired ponds as measured by drop cylinder at 1 and 20 m from the grass edge.

To summarize, the pond having the greater average catch (from Table 11) is shown below, by gear and year.

	Before enclosure		After enclosure	
Year	Pond with more	Significant?	Pond with more	Significant?
Brown shrimp - otter trawl				
1	21% more in no weir	No	72% more in no weir	No
2	75% more in natural	No	176% more in natural	Yes
Brown shrimp - drop cylinder				
2			292% more in natural	Yes
White shrimp - otter trawl				
1	3% more in no weir	No	136% more in natural	No
2	22% more in natural	No	17% more in natural	No
White shrimp - drop cylinder				
2			40% more in no weir	No

The traps and screens in the unweired pond had no effect on brown shrimp in one year but did in the second year. White shrimp were probably affected in one year but not the other, as well.

Discussion

Densities of both penaeid shrimp species were usually reduced behind the weir (Figures 12, 13, 15, and 16). Surface trawl catches of both species, beam trawl catches of brown shrimp (Bradshaw 1985) and white shrimp, and results from drop cylinder sampling further verify this conclusion. Lower densities of shrimp probably resulted from reduced immigration of postlarval and juvenile shrimp past the weir.

The probable faster growth and lower mortality of brown shrimp (Chapter III) and faster white shrimp growth (Chapter IV) behind the weir may have been the result of lower densities causing reduced intraspecific competition.

Rogers et al. (1987) found that the number of shrimp emigrating from behind a standard, fixed-crest weir was less than half as much as the number from behind a slotted weir. This was likely a direct result of improved access for immigration of small shrimp into the slotted-weir pond. They found that trawling indices of brown shrimp abundance were not significantly different between a pond having a slotted weir and one with a standard weir. (Their conclusion about greater brown shrimp export from the slotted-weir pond as compared to a weired pond, however, was based on trap catches resulting, they hypothesized, from faster turnover rates in the slotted-weir pond.) Assuming mortality was equal, and since standing stock was equal, the only way more shrimp could have emigrated from the slotted-weir pond was if immigration was greater. I generally conclude, therefore, that the primary mechanism of reduced shrimp export from behind a weir is reduced immigration of postlarvae and small juveniles.

I found, from otter trawl catches, slight possible reductions in standing stock densities of penaeid shrimp in the open, experimental (unweired) ponds relative to a nearby natural pond but, from drop cylinder sampling, that brown shrimp were usually more abundant in the natural pond than in the unweired pond. I did not find any density differences in white shrimp between the two habitat types with drop cylinder sampling. Because of this, I believe it is reasonable to

consider the shrimp export (not to be confused with production, which includes emigration plus mortality) values determined by Herke et al. (1987a) conservative estimates of the usual amounts of shrimp emigrating from shallow marsh waters toward the Gulf of Mexico and were more conservative for brown shrimp than whites.

Rogers et al. (1987) found standing stock densities of brown shrimp to be greatest in the natural pond, less in a pond having a slotted weir, and the least in a pond having a solid (unslotted) weir. I found that brown shrimp standing stock densities in an open, experimental pond were somewhere between those of the totally unaltered pond and one having a slotted weir.

Herke et al. (1987a) measured the following numbers and weights of penaeid shrimp emigrating from the 26.5 ha of open water in the unweired study pond.

Species	1983	1984	Average annual emigration per ha
		Numbers	
Brown shrimp	316,475	286,064	11,369
White shrimp	256,046	320,116	10,871
		Kilograms	
Brown shrimp	839.7	857.8	32.02
White shrimp	722.6	792.8	28.59

These actual measurements of shrimp export are in the range of previous estimates. Sullivan (1985) used matk and recapture to estimate standing stocks of 5,709 to 17,933 brown shrimp per hectare

in coastal Texas ponds. Rose et al. (1975) harvested 48.2 kg/ha of mostly brown shrimp during one season from a naturally stocked, small Louisiana impoundment from which large predators had been excluded by a 13-mm mesh screen.

The question arises as to how the shrimp export data from Herke et al. (1987a) could be applied in shrimp management. To evaluate shrimp habitat and estimate shrimp abundance, it is important to recognize conditions influencing shrimp densities. Some of these are the effect of marsh edge relative to area of open water, distance from the Gulf of Mexico, and accessibility. Because there were no replications of weired, unweired, or natural ponds, results from this work cannot be applied to the average marsh. They do, however, provide relative magnitudes of shrimp abundance in these habitats.

Density might also be useful in determining relative value of marsh being considered for alteration through dredge and fill, draining, or impoundment. For example, there is interest in using coastal Louisiana marshes for intensive mariculture. Rose et al. (1975) estimated 141.2 kg/ha of wild shrimp were harvested in one season from an impoundment where predators had been removed and 48.2 kg/ha from an impoundment where predators had been excluded but not otherwise controlled. The impoundments were off Bayou Jean Lacroix near Houma. Herke et al. (1987a) measured 60.6 kg/ha of shrimp emigrating naturally from a marsh pond containing predators. Since 301.3 kg/ha of other commercially important and forage species emigrated from the same natural areas simultaneously with the shrimp (Herke et al. 1987a), it is clear that coastal marshes should not be

used for single-species mariculture.

Conclusions

1. The weir may have reduced the catches (density) of brown shrimp.
2. There were fewer white shrimp behind the weir than in a pond with no weir.
3. I theorize that the primary mechanism for reduced export of shrimp from weired marshes is reduced immigration of postlarvae and small juveniles.
4. The experimental conditions of the screens and traps in the channels leading to and from the pond with no weir probably had some influence on the densities of brown shrimp observed there.
5. There was only a small chance of decreased abundance due the effect of the traps and screens on white shrimp densities in the ponds having no weirs.
6. Measurements of numbers and weight of shrimp from the open experimental ponds by Herke et al. (1987a) can be considered reasonable, although conservative, estimates of brown shrimp and white shrimp emigrating toward the Gulf of Mexico per hectare of marsh water in coastal Louisiana.

CHAPTER VI. Relation between juvenile white shrimp emigration and environmental variables in a coastal Louisiana marsh pond.

INTRODUCTION

Zein-Eldin and Renaud (1986) reviewed and summarized existing knowledge of environmental effects on white shrimp and concluded that effects of salinity and other environmental variables were only partially understood. Water-control structures constructed in marsh waterways further complicate shrimp ecology (Herke et al. 1987a; Knudsen et al. 1989; Chapters III, IV, and V). Shrimp ecology should be considered when designing and managing structures so adverse effects on shrimp can be minimized. I therefore decided to use trap and environmental data from Herke et al. (1987b) to conduct further investigations on how environmental variables influence abundance and emigration patterns of juvenile white shrimp.

White shrimp are generally tolerant of wide salinity ranges (Zein-Eldin and Renaud 1986). Yet, as shrimp grow in coastal marshes, they eventually migrate toward the Gulf of Mexico. This migration may be size-dependent, and thus act to "bleed off" larger individuals as it apparently does for brown shrimp (Herke 1971; Wicker et al. 1988; Chapter III). White shrimp size at emigration varies between years (Chapter IV). Herke (1971) further hypothesized that shrimp emigrate in response to external stimuli and increase in size. Sharp declines in water temperature are most influential in white shrimp emigration (Lindner and Anderson 1956; Gaidry and White 1973; Rogers and Herke 1985b; Chapter IV). However, since temperature is not influential under all circumstances, it is likely that a number of other variables

operate singly or synergistically with temperature in influencing emigration.

Initial investigations with multiple regression models of brown shrimp emigration resulted in relatively weak models (Knudsen 1986). Further work using entropy data analysis produced somewhat better results (Chen et al. 1987). Regression analysis on potential environmental cues for Atlantic croaker (*Micropogonias undulatus*) migration resulted in relatively weak models as well (Herke et al. 1987b). Because of the deficiencies of these three projects, I thought that conceptually modeling the problem perhaps would best be done by a combination of complementary techniques. This is because no one approach can completely describe the dynamics of complex interrelations. For example, regression models describe synchronous cyclic phenomena well, but are inadequate to account for the occasional extreme value which, after surpassing some environmental tolerance limit for the organism, stimulates massive changes in biological systems.

The objectives, then, were to evaluate the effects of environmental variables on white shrimp emigration and develop a predictive model describing the relation of environmental stimuli to shrimp movements. The goal of this work was to provide marsh managers with an improved description of conditions under which structures should be opened to allow white shrimp to emigrate.

METHODS

Environmental effects on numbers emigrating

The daily catch data of white shrimp from the Cameron-Creole study (Herke et al. 1987a,b) was the dependent variable in this portion of my work. In Herke et al. (1987a,b), all emigrating organisms too large to pass through the 1/4-in mesh were captured in identical traps. The traps were fished continuously from February 1983 to February, 1985. The number of shrimp captured each day was recorded. Refer to Chapter II and Herke et al. (1987a,b) for further details on the trapping methods at the paired ponds. I limited my analyses to catch and environmental data from the unweired ponds because they theoretically best reflect what might be encountered in a completely natural system.

During the Cameron-Creole study (Herke et al. 1987a,b), a variety of continuously recording instruments collected hourly observations of water temperature, salinity, pH, dissolved oxygen, water velocity, and water level. Daily precipitation was monitored locally; barometric pressure and wind speed were obtained from the National Weather Service at Lake Charles, 25.5 km to the north. These observations were reduced to daily mean, minimum, and maximum for relation with daily trap catches. A large number of derived variables, thought to potentially influence shrimp emigration, were also calculated from these initial measurements. For example, volume of inflow and outflow was derived from water velocity and water level. Furthermore, for every basic variable, the daily mean, maximum, and minimum values were lagged one and two days, and the change in each mean, maximum, and minimum from one day to the next was calculated. This resulted in 109

variables.

Graphic analysis.- To begin the analysis, I reduced the data to cover the periods during which white shrimp are generally present in the marsh, 6 July to 18 December 1983 and 1984. I then plotted white shrimp catches, as indicative of emigration, together with all measured environmental variables. Since no clear conclusions could be reached, I decided to further explore the data statistically.

Correlations.- First, I produced correlations between the natural log of total number of shrimp emigrating daily and environmental variables potentially influencing emigration using SAS (SAS Institute 1988a). Because I needed to reduce the 109 independent variables to a more manageable number, and since many of the 109 variables were derived from original measurements and therefore highly correlated with each other and redundant, I first ran correlations between the dependent variable natural log of daily catch and all 109 variables. I then selected only those variables having a correlation coefficient greater than 0.30, as well as at least one of the measured or derived variables representing every class (e.g., temperature, salinity, etc.) of environmental factors, to consider as possibly correlated with emigration and to submit later to stepwise multiple regression.

Of course, several other density-dependent variables, particularly competition for food and space, may also influence emigration but these were not measured. I tried to simulate the effect of space by creating a variable simulating the seasonal density of shrimp. This was done by adding day of the year, and day of year squared, to the model. There

was no way to index food availability.

After initial runs on the 6 July - 18 December period, poor correlations prompted me to investigate whether correlations might be improved by breaking the white shrimp season into summer and fall since it was generally suspected that fall emigration is weather-induced while summer emigration may not be. I used September 25 as the cut-off.

Stepwise Multiple Regression.- I used PROC REG (SAS Institute 1988a) with a forward stepwise procedure to further evaluate the importance of considering variables together. The model was run independently for 1983 and 1984, for the fall only. The final model took the form

$$LN(Catch) = a(VAR1) + b(VAR2) + \ldots . m(VARn) + Error.$$

To test the fit of this model, and investigate its potential as a predictive model, I used the 1983 model to predict 1984 catch and vice versa. The predicted and actual catches were plotted for comparison.

Superposed Epoch Analysis.- Because it is possible that, for a given environmental variable, some single, extreme environmental events may trigger emigration even though that variable may or may not otherwise be important, a method to help determine the significance of such phenomena was needed. Because linear models depend on a direct relationship between the dependent and independent variables over time, they cannot detect significance of single events. I followed the methods of Prager and Hoenig (1990), who first applied superposed epoch analysis to fisheries. I performed all computations described below with SAS (SAS Institute 1988b,c).

Superposed epoch analysis is a non-parametric method whereby the dependent variable daily catch, on days of extreme environmental events (key event), is compared to daily catch from the immediately surrounding days. The key events were determined by reviewing a variety of independent environmental variables and selecting, for each variable, those days upon which there was either an extreme change since the previous day or the variable was extremely high or low. An observation or a change in a variable was considered to be extreme if it was greater than $\pm$ 1.5 standard deviations from the mean of all observations or all changes in that variable over the season. I examined the effects of extreme values or changes in salinity, temperature, barometric pressure, water flow, rainfall, pH, and dissolved oxygen using epoch analysis. Several variables, such as salinity and temperature, could not be examined for effects of extremely high or low values (although they were tested for drastic changes from one day to the next) because those values were often concentrated in at least several-day periods of extreme cold or heat, high or low salinity, respectively. Superposed epoch analysis only works well when extreme environmental events are independent of the surrounding observations.

Once key events were identified for each independent variable, a superposed epoch was constructed. This was done by creating a matrix containing the dependent variable values, the rows of which represented key events and five columns representing two days prior to the key event, the key event day, and two days following the key event (the days surrounding the key event are referred to as background

days). The mean of the dependent variable on background days was then compared to the mean on key event days using the statistic

$$W = (\bar{d} * N_B^{1/2}) \; / \; S_w$$

where W is an index of the difference in catch on all key days relative to all background days, S_w is a measure of dispersion (defined below), N_B is the total number of background days, and d is the mean of all paired differences between the natural log of daily catch on key event days and the mean on background days. This is expressed as

$$\bar{d} = 1 \; / \; N_B \sum_{i=1}^{N_E} \sum_{j=1}^{n_i} (E_i - B_{ij})$$

where n_i is the number of background catch values for key day i, E_i are the natural logs of daily catches on key days and B_{ij} are the logs of daily catches for each corresponding background day.

S_w is computed similarly to a paired *t*-test as

$$S_w = \frac{1}{N_B - 1} \sum_{i=1}^{N_E} \sum_{j=1}^{n_i} \left[(E_i - B_{ij} - \bar{d})^2 \right]^{1/2}$$

Because I could not determine where the test statistic W fell in relation to the distribution of all possible values of W using a statistical table, it was necessary to generate the null distribution of a large number of randomly generated W values from the data in question using Monte Carlo simulation. If x of the v randomly generated W values were larger than the observed W, the estimated probability P of the observed W would be (x+1)/(v+1) (Prager and Hoenig 1989). The program to perform Monte Carlo trials was iterated

until P stabilized. I found that P stabilized sufficiently with 1500 iterations. Then the test statistic was compared to the null distribution and if it fell below the 0.05 percentile, I rejected the null hypothesis. The null hypothesis took the form

H_o: There is no association between dramatic decreases, increases, highs, or lows in a given environmental variable and daily catch of white shrimp.

The alternate hypothesis took the form

H_a: White shrimp emigration was less (or greater) on days of dramatic decreases, increases, highs, or lows in a given environmental variable.

Variables for salinity, water temperature, barometric pressure, outward and inward flow, dissolved oxygen, pH, and rainfall were tested with epoch analysis.

Length at emigration

Although previous research has suggested that any potential emigration response to environmental stimuli may be size-dependent (Herke 1971), definitive conclusions are yet to be made. I investigated this question by four approaches: 1) Mean daily white shrimp length at emigration was plotted against environmental variables to observe whether environmental events triggered emigration of certain sizes. 2) the number of emigrants was plotted versus mean length to observe whether the size of emigrants was related to the magnitude of the stimulus for emigration. Mean length and total catch were also plotted over time to see whether emigration peaks coincided with noticeable changes in daily mean length of emigrants. 3) the

number of emigrants was plotted versus variation in daily lengths of emigrants to determine whether, on days of mass emigration, that exodus occurred for shrimp of a wider range of sizes. 4) I used linear regression to test the hypothesis that size at emigration did not change over the period of emigration; since the shrimp were known to be growing, no change in the size at emigration would validate the hypothesis that white shrimp emigration is a "bleeding-off" of individuals as they attain a certain size.

Results

Environmental effects on numbers emigrating

Because information from each statistical approach is complementary, results for each environmental variable are considered together (below). Of the 109 environmental variables submitted for correlation with natural log of white shrimp catch, none had a correlation coefficient greater than $|0.68|$, although many coefficients were equal or greater than $|0.30|$ (Tables 12-14). Many of the variables were redundant, however. Date and date squared were always positively correlated with log of catch; this was apparently due to the seasonal trend of greater catches later in the season.

In general, correlation between white shrimp catch and individual environmental variables over the entire season of marsh presence did not explain daily variation in catches. In some cases, seasonal changes in emigration were partially explained by seasonal changes in environmental variables but that does not help with the goals of management. This is because a gradual, seasonal increase in an environmental variable may be generally associated with a gradual,

Table 12. Correlation coefficients (in descending order) between natural log of total daily catch of white shrimp and environmental variables.

1983		1984	
Variable	r	Variable	r
Date	0.60	Maximum air temp. yesterday	0.40
Date squared	0.56	Minimum water temp. yesterday	0.40
Minimum salinity	0.51	Mean water temp. yesterday	0.40
Maximum salinity yesterday	0.49	Mean air temp. yesterday	0.39
Mean salinity	0.48	Maximum water temp. yesterday	0.38
Maximum salinity 2 days ago	0.48	Dewpoint yesterday	0.38
Mean salinity yesterday	0.48	Minimum salinity	0.37
Maximum salinity	0.46	Maximum salinity yesterday	0.37
Minimum salinity yesterday	0.46	Mean salinity	0.37
Mean salinity 2 days ago	0.45	Maximum air temp. 2 days ago	0.37
Minimum air temperature	-0.45	Minimum air temp. 2 days ago	0.37
Minimum water temperature	-0.44	Minimum salinity 2 days ago	0.36
Minimum salinity 2 days ago	0.43	Mean air temperature	0.36
Mean air temperature	-0.42	Maximum air temperature	0.36
Mean water temperature	-0.41	Mean salinity 2 days ago	0.35
Mean air temp. 2 days ago	-0.41	Minimum dissolved oxygen 2 days ago	-0.35
Minimum air temp. 2 days ago	-0.40	Maximum pH	-0.35
Maximum air temp. 2 days ago	-0.40	Maximum dissolved oxygen 2 days ago	-0.35
Dewpoint	-0.40	Mean salinity yesterday	0.35
Mean water temp. 2 days ago	-0.39	Maximum salinity 2 days ago	0.35
Maximum air temp. 2 days ago	-0.39	Maximum water temperature	0.34
Minimum water temp. 2 days ago	-0.38	Mean water temp. 2 days ago	0.34
Maximum water temperature	-0.38	Minimum water temp. 2 days ago	0.34
Minimum water temperature yesterday	-0.38		

Continued.

Table 12. Continued.

1983		1984	
Variable	r	Variable	r
Mean water temp. yesterday	-0.37	Mean dissolved oxygen yesterday	-0.34
Maximum water temp. yesterday	-0.36	Dewpoint	0.34
Maximum air temperature	-0.36	Maximum dissolved oxygen	-0.34
Minimum air temp. yesterday	-0.35	Minimum air temperature	0.34
Volume of inflow	-0.35	Mean dissolved oxygen 2 days ago	-0.33
Dewpoint 2 days ago	-0.35	Mean dissolved oxygen	-0.33
Mean air temp. 2 days ago	-0.35	Mean water temperature	0.33
Duration of inflow	-0.34	Minimum dissolved oxygen	-0.33
Mean pH 2 days ago	0.34	Mean air temp. 2 days ago	0.33
Maximum air temp. yesterday	-0.32	Minimum salinity yesterday	0.33
Duration of outflow	0.32	Minimum dissolved oxygen 2 days ago	-0.33
Mean pH yesterday	0.31	Minimum water temperature	0.32
Mean pH	0.31	Maximum water temperatue 2 days ago	0.32
Mean dissolved oxygen	0.31	Maximum dissolved oxygen yesterday	-0.32
Maximum dissolved oxygen	0.30	Date squared	-0.32
		Maximum salinity	0.31
		Barometric pressure yesterday	-0.28

Table 13. Correlation coefficients (in descending order) between natural log of total daily catch of white shrimp and environmental variables during summer (6 July - 24 September).

1983		1984	
Variable	r	Variable	r
Mean salinity 2 days ago	0.54	Minimum salinity 2 days ago	0.41
Maximum salinity 2 days ago	0.53	Mean salinity 2 days ago	0.40
Minimum salinity 2 days ago	0.49	Maximum salinity 1 day ago	0.39
Minimum salinity 1 day ago	0.46	Maximum salinity 2 days ago	0.39
Mean salinity 1 day ago	0.45	Mean salinity 1 day ago	0.38
Minimum water temp 1 day ago	-0.45	Minimum salinity 1 day ago	0.38
Minimum water temperature	-0.44	Maximum salinity	0.35
Maximum salinity 1 day ago	0.43	Mean salinity	0.34
Minimum water temp 2 days ago	-0.42	Minimum salinity	0.34
Minimum salinity	0.41	Volume of outflow 1 day ago	0.32
Mean water temp 1 day ago	-0.41	Volume of inflow 2 days ago	0.32
Mean water temperature	-0.39	Volume of outflow 2 days ago	0.28
Maximum air temp 2 days ago	-0.39	Maximum dissolved oxygen 2 days ago	-0.26
Mean water temp 2 days ago	-0.39		
Mean air temperature	-0.37		
Minimum water temperature	-0.37		
Mean salinity	0.36		
Mean air temp 2 days ago	-0.36		
Maximum water temp 1 day ago	-0.34		
Maximum water temperature	-0.34		
Maximum salinity	0.34		
Mean air temp 1 day ago	-0.34		
Maximum air temp 1 day ago	-0.33		
Maximum water temp 2 days ago	-0.31		
Maximum air temperature	-0.31		
Dewpoint	-0.31		
Barometric pressure 2 days ago	-0.30		
Minimum air temp 1 day ago	-0.30		
Mean outward velocity	0.29		
Minimum air temp 2 days ago	-0.27		

Table 14. Correlation coefficients (in descending order) between natural log of total daily catch of white shrimp and environmental variables during autumn (25 September - 18 December).

1983		1984	
Variable	r	Variable	r
Volume of inflow	-0.55	Maximum pH	-0.68
Change in inflow since yesterday	-0.50	Mean pH yesterday	-0.57
Duration of inflow	-0.48	Mean pH	-0.56
Change in duration of inflow since yesterday	-0.48	Maximum pH yesterday	-0.56
Change in minimum water temp since yesterday	-0.45	Minimum pH yesterday	-0.54
Duration of outflow	0.45	Maximum pH 2 days ago	-0.53
Mean inward velocity	-0.44	Maximum air temp yesterday	0.47
Change in mean inward velocity since yesterday	-0.44	Mean water temp yesterday	0.46
Change in duration of outflow since yesterday	0.39	Maximum water temp yesterday	0.46
dewpoint yesterday	0.38	Mean pH 2 days ago	-0.45
Volume of outflow	-0.37	Minimum water temp yesterday	0.45
Maximum dissolved oxygen yesterday	-0.37	Minimum pH	-0.44
Mean air temp yesterday	0.33	Mean air temp yesterday	0.44
Mean water temp yesterday	0.32	Minimum dissolved oxygen yesterday	-0.43
Mean diss oxygen yesterday	-0.32	Maximum salinity yesterday	0.42
Change in mean diss oxygen since yesterday	0.32	Maximum air temp 2 days ago	0.40
Change in minimum salinity since yesterday	0.32	Dewpoint yesterday	0.40
Minimum air temp yesterday	0.32	Mean dissolved oxygen	-0.40
Maximum water temp yesterday	0.31	Maximum dissoved oxygen	-0.39
		Mean inward velocity	-0.39
		Mean dissolved oxygen yesterday	-0.39
		Maximum air temperature	0.39
		Maximum salinity 2 days ago	0.39
		Mean air temperature	0.38
		Minimum dissolved oxygen	-0.38

Continued.

Table 14. Continued.

1983		1984	
Variable	r	Variable	r
Change in mean water temp since yesterday	-0.31	Minimum air temp yesterday	0.38
Minimum water temp yesterday	0.31	Mean water temp 2 days ago	0.38
Maximum air temp yesterday	0.30	Maximum water temp 2 days ago	0.38
Barometric pressure yesterday	-0.30	Mean salinity	0.37
		Minimum water temperature	0.36
		Minimum pH 2 days ago	-0.36
		Minimum air temperature	0.35
		Volume of inflow	-0.34
		Mean dissolved oxygen 2 days ago	-0.34
		Mean air temp 2 days ago	0.34
		Dewpoint	0.33
		Minimum dissolved oxygen 2 days ago	-0.33
		Mean water temperature	0.33
		Mean salinity 2 days ago	0.33
		Maximum salinity	0.32
		Maximum dissolved oxygen yesterday	-0.32
		Mean salinity yesterday	0.32
		Precipitation	0.32
		Minimum salinity	0.31
		Maximum dissolved oxygen 2 days ago	-0.31
		Precipitation yesterday	0.31
		Minimum water temeprature	0.30
		Barometric pressure yesterday	-0.26

seasonal increase in shrimp emigration, resulting in a relatively strong correlation. However, to investigate stimuli to emigration, I was trying to detect short-term events. Correlation is effective for this if their is a synchronous cycling of emigration with a given environmental variable.

When I used stepwise regression with a variety of variables, I obtained models with nine variables in both 1983 and 1984 (Table 15). Of the nine variables, dissolved oxygen, pH, salinity, and lunar cycle appeared in both models. Neither of the models provided very good explanation of variation (r^2 = 0.70 and 0.65, in 1983 and 1984 respectively). Models from each year were poor predictors of catch in the other year (Figure 26). The relation between predicted and actual catch for 1983 was barely significant (P = 0.0402, r^2 = 0.05) while the relation for 1984 was not significant (P = 0.1391, r^2 = 0.03).

Salinity.- White shrimp emigration often appeared to be inversely related to salinity (Figure 27). The pattern was not entirely consistent but is discernible. A number of salinity variables exhibited positive correlation with daily catch of emigrants ($r > |0.30|$); minimum salinity had the strongest relation in both years (r = 0.51 in 1983, r = 0.37 in 1984) (Table 12). This positive correlation resulted from a general seasonal trend, however, and not from a coincidental cycling (Figure 27). Correlation was positive in summer of 1983 and 1984, the best fit exhibited by mean salinity 2 days prior in 1983 and by minimum salinity 2 days prior in 1984 (r = 0.54 and 0.41, respectively) but this again was primarily related to coincidental seasonal trends (Table 13, Figure 27). There was no

Table 15. Results of stepwise linear regression of a number of environmental variables on the natural log of daily white shrimp catch.

Variable	Parameter estimate	Prob > F
1983		
Intercept	-6.2632	0.1088
Mean salinity	0.2057	0.0010
Volume of inflow	-0.0001	0.0001
Maximum salinity 1 day ago	-0.9844	0.0642
Minimum air temp 1 day ago	0.1162	0.0001
Maximum pH	1.7076	0.0008
Maximum dissolved oxygen 1 day ago	-0.3322	0.0466
Lunar cycle peaking on full moon	-0.0284	0.0001
Lunar cycle peaking on new and full moons	0.0045	0.0532
Mean outward water velocity	-0.1189	0.0003
1984		
Intercept	44.9104	0.0001
Change in minimum water temp since yesterday	-0.1812	0.0123
Maximum salinity 2 days ago	0.1216	0.0005
Mean pH 2 days ago	-1.8579	0.0302
Precipitation 1 day ago	0.3274	0.0130
Minimum dissolved oxygen 1 day ago	-0.4345	0.0001
Maximum pH	-2.5536	0.0002
Dewpoint 2 days ago	-0.1541	0.0001
Lunar cycle peaking on full moon	-0.0201	0.0001
Lunar cycle peaking on new and full moons	0.0046	0.0834

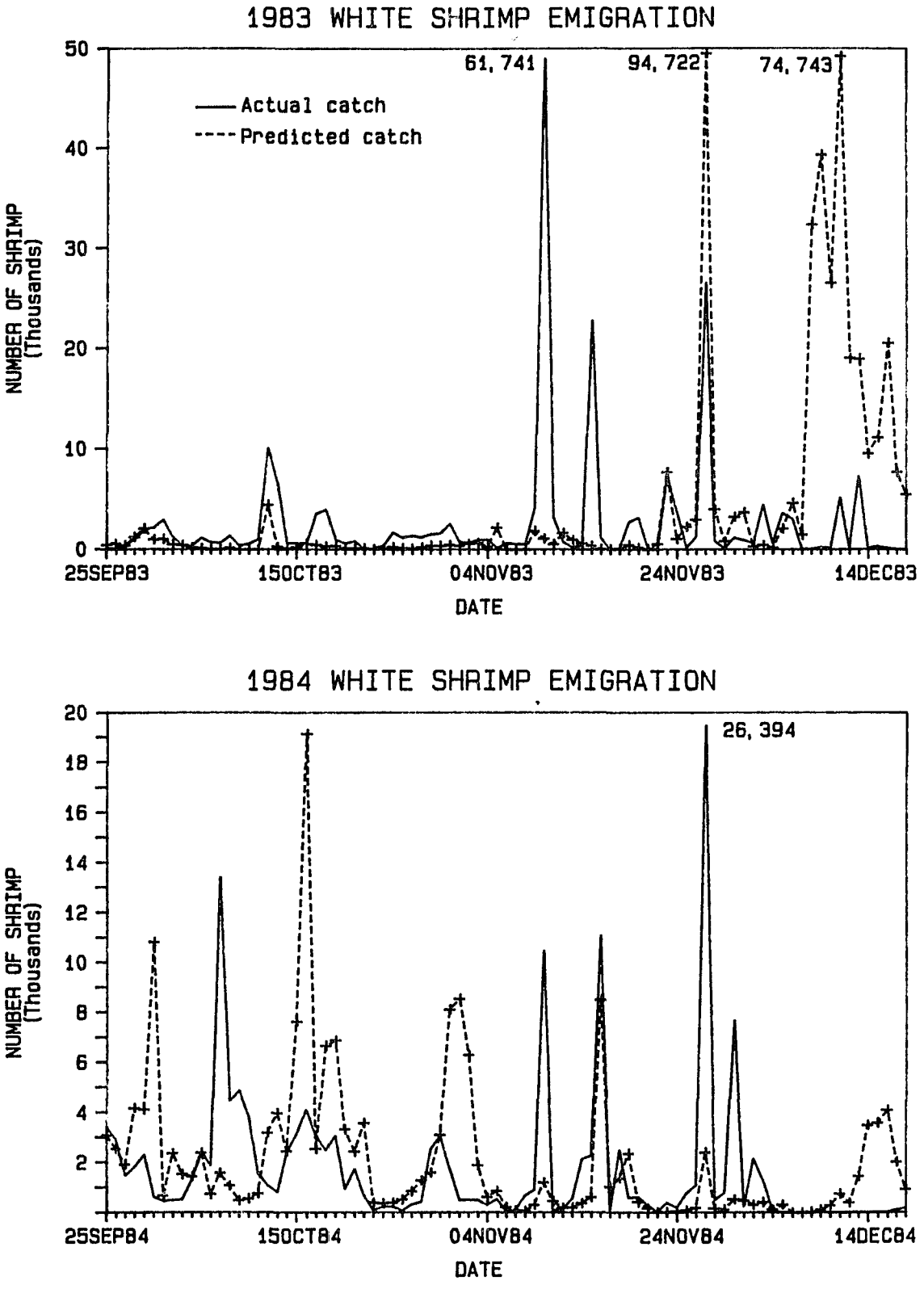


Figure 26. Actual versus predicted white shrimp emigration trap catches using model derived from the other year.

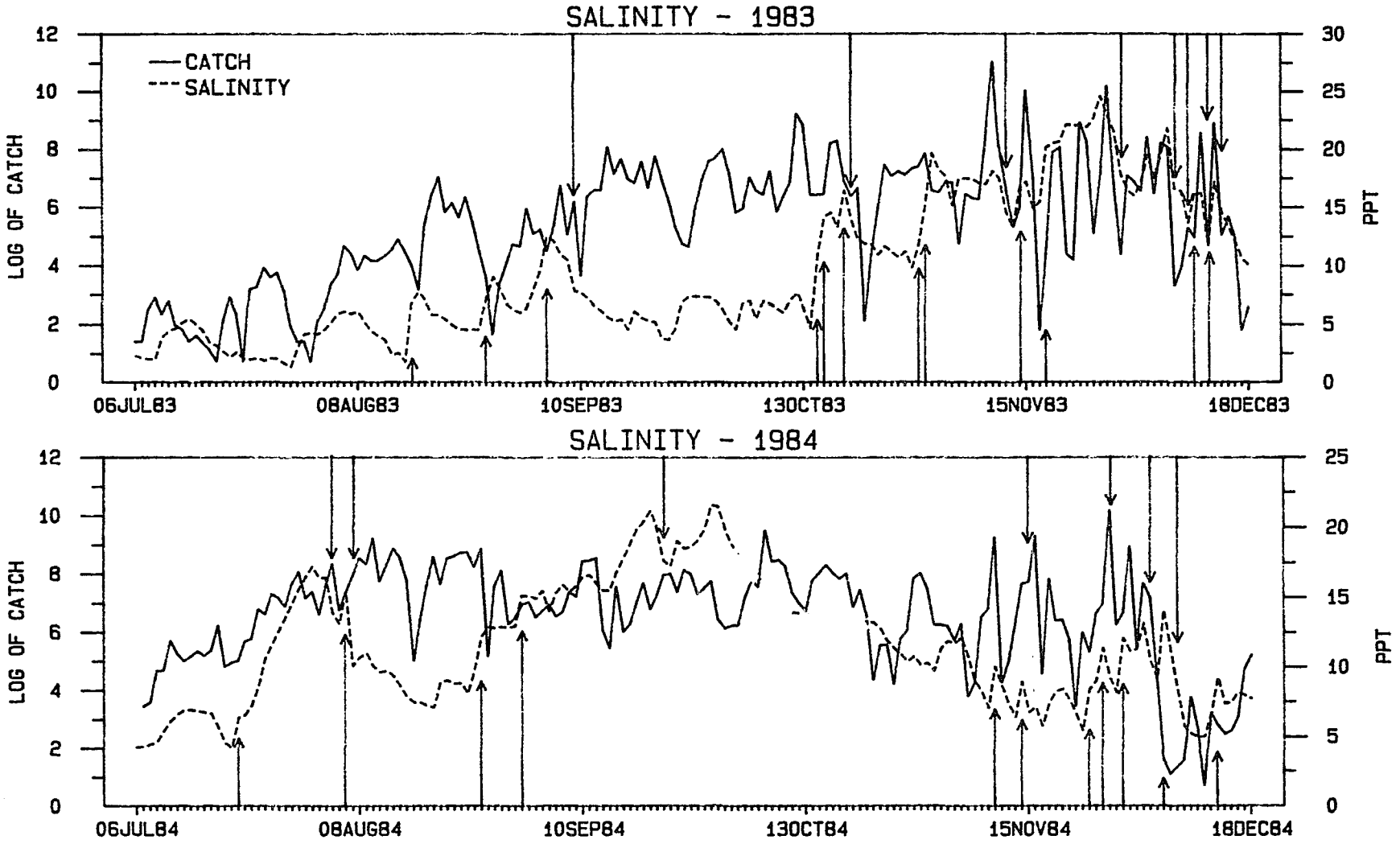


Figure 27. Natural log of white shrimp catch and salinities in 1983 and 1984. Arrows indicate key days on which salinity decreased (down) or increased (up) dramatically.

relation between salinity and emigration in fall, 1983 but several salinity variables had a positive correlation in fall, 1984, maximum salinity had the strongest relation of those ($r = 0.42$, Table 14).

From epoch analysis I found that single-day, dramatic decreases in salinity resulted in significantly smaller catches in 1983 but significantly greater catches in 1984 (Table 16, Figure 27). Because of the conflicting results, I could make no firm conclusions about the effects from salinity decreases. There was no significant emigration of white shrimp with dramatic increases in salinity.

Figure 28 provides a good illustration of epoch analysis results. In that figure, individual lines represent the log of catch for the 2 days preceding the key event (dramatic decrease or increase in salinity), the catch on the key event day, and the catch for 2 days following the key event. The histograms represent the mean of catch for all key events. In the top panel, it can be seen that, in 1983, the mean catch on the key event days was lower than on the preceding and subsequent background days but in 1984 the mean catch was highest on key event days. In the bottom panel, the lack of difference in catch on salinity increase key event days and surrounding background days is evident.

Temperature.- In 1983, catch was negatively correlated with minimum air temperature, among other temperature variables, over the entire season ($r = -0.45$, Table 12). This may have been due partly to relatively large catches being associated with decreases in temperature (Figure 29) but was probably also due partly to an inverse seasonal relationship between temperature and catch. Minimum water temperature 1

Table 16. Results of superposed epoch analysis for effects of dramatic changes in environmental variables on daily white shrimp emigration from the unweired pond in 1983 and 1984. Null hypothesis is that environmental variables have no influence on catch.

Effect	Year	W	P	Alternate hypothesis
Salinity				
Decrease since yesterday	1983	-2.7374	0.0373 *	Smaller catches
Decrease since yesterday	1984	3.5769	0.0060 **	Larger catches
Increase since yesterday	1983	-1.5113	0.1706	
Increase since yesterday	1984	0.7811	0.3011	
Water Temperature				
Decrease since yesterday	1983	2.7289	0.0499 *	Larger catches
Decrease since yesterday	1984	4.2147	0.0053 **	Larger catches
Increase since yesterday	1983	-2.3081	0.0633	
Increase since yesterday	1984	2.3766	0.0653	
Barometric Pressure				
Decrease since yesterday	1983	0.4925	0.3837	
Decrease since yesterday	1984	-0.7763	0.3271	
Increase since yesterday	1983	3.2899	0.0246 *	Larger catches
Increase since yesterday	1984	1.2966	0.2079	
Decrease 1 day ago	1983	2.7861	0.0326 *	Larger catches
Decrease 1 day ago	1984	2.3475	0.0673	
Increase 1 day ago	1983	-2.2565	0.0686	
Increase 1 day ago	1984	-2.7105	0.0480 *	Smaller catches

Table 16. Continued.

Effect	Year	W	P	Alternate hypothesis
Barometric Pressure				
Decrease tomorrow	1983	-4.2356	0.0027 **	Smaller catches
Decrease tomorrow	1984	-3.1470	0.0173 *	Smaller catches
Increase tomorrow	1983	4.6739	0.0027 **	Larger catches
Increase tomorrow	1984	1.8247	0.1206	
Low during past 24 hours	1983	4.5936	0.0020 **	Larger catches
Low during past 24 hours	1984	1.0086	0.2545	
High during past 24 hours	1983	-2.0833	0.0933	
High during past 24 hours	1984	-1.5394	0.1379	
Inward Flow				
Low during past 24 hours	1983	6.2281	0.0007 **	Larger catches
Low during past 24 hours	1984	3.4645	0.0166 *	Larger catches
High during past 24 hours	1983	-4.54631	0.0040 **	Smaller catches
High during past 24 hours	1984	-1.42174	0.1799	
Decrease since yesterday	1983	3.3872	0.0186 *	Larger catches
Decrease since yesterday	1984	1.8953	0.1286	
Increase since yesterday	1983	-4.6139	0.0006 **	Smaller catches
Increase since yesterday	1984	-1.2977	0.1925	
Outward Flow				
Low during past 24 hours	1983	-2.4476	0.0366 *	Smaller catches
Low during past 24 hours	1984	-1.5888	0.1346	

Continued.

Table 16. Continued

Effect	Year	W	P	Alternate hypothesis
Outward flow				
High during past 24 hours	1983	4.6791	0.0033 **	Larger catches
High during past 24 hours	1984	2.8349	0.0393 *	Larger catches
Decrease since yesterday	1983	-0.6330	0.3378	
Decrease since yesterday	1984	-2.7868	0.0440 *	Smaller catches
Increase since yesterday	1983	1.9449	0.1159	
Increase since yesterday	1984	1.4877	0.1825	
Low 1 day ago	1983	-2.4094	0.0613	
Low 1 day ago	1984	0.2963	0.4151	
High 1 day ago	1983	1.0835	0.2812	
High 1 day ago	1984	-1.6705	0.1486	
Rainfall				
During past 24 hours	1983	1.2043	0.2338	
During past 24 hours	1984	0.5032	0.3584	
Yesterday	1983	1.1786	0.2478	
Yesterday	1984	4.1518	0.0040 **	Larger catches

Continued.

Table 16. Continued.

Effect	Year	W	P	Alternate hypothesis
Dissolved Oxygen				
Decrease since yesterday	1983	-0.1304	0.5423	
Decrease since yesterday	1984	-0.8679	0.2678	
Increase since yesterday	1983	2.4994	0.0733	
Increase since yesterday	1984	-0.3327	0.4064	
Decrease tomorrow	1983	-0.9717	0.2759	
Decrease tomorrow	1984	0.0156	0.5236	
Increase tomorrow	1983	3.5083	0.0166 *	Larger catches
Increase tomorrow	1984	2.2288	0.0839	
Low during past 24 hours	1983	0.8980	0.3038	
Low during past 24 hours	1984	-0.8209	0.2925	
High during past 24 hours	1983	-0.5958	0.3251	
High during past 24 hours	1984	-1.1593	0.2152	
Low tomorrow	1983	1.9633	0.1166	
Low tomorrow	1984	-1.0478	0.2572	
High tomorrow	1983	3.6866	0.0087 **	Larger catches
High tomorrow	1984	1.2239	0.2012	

* Significant ($P < 0.05$)
** Highly significant ($P < 0.01$)

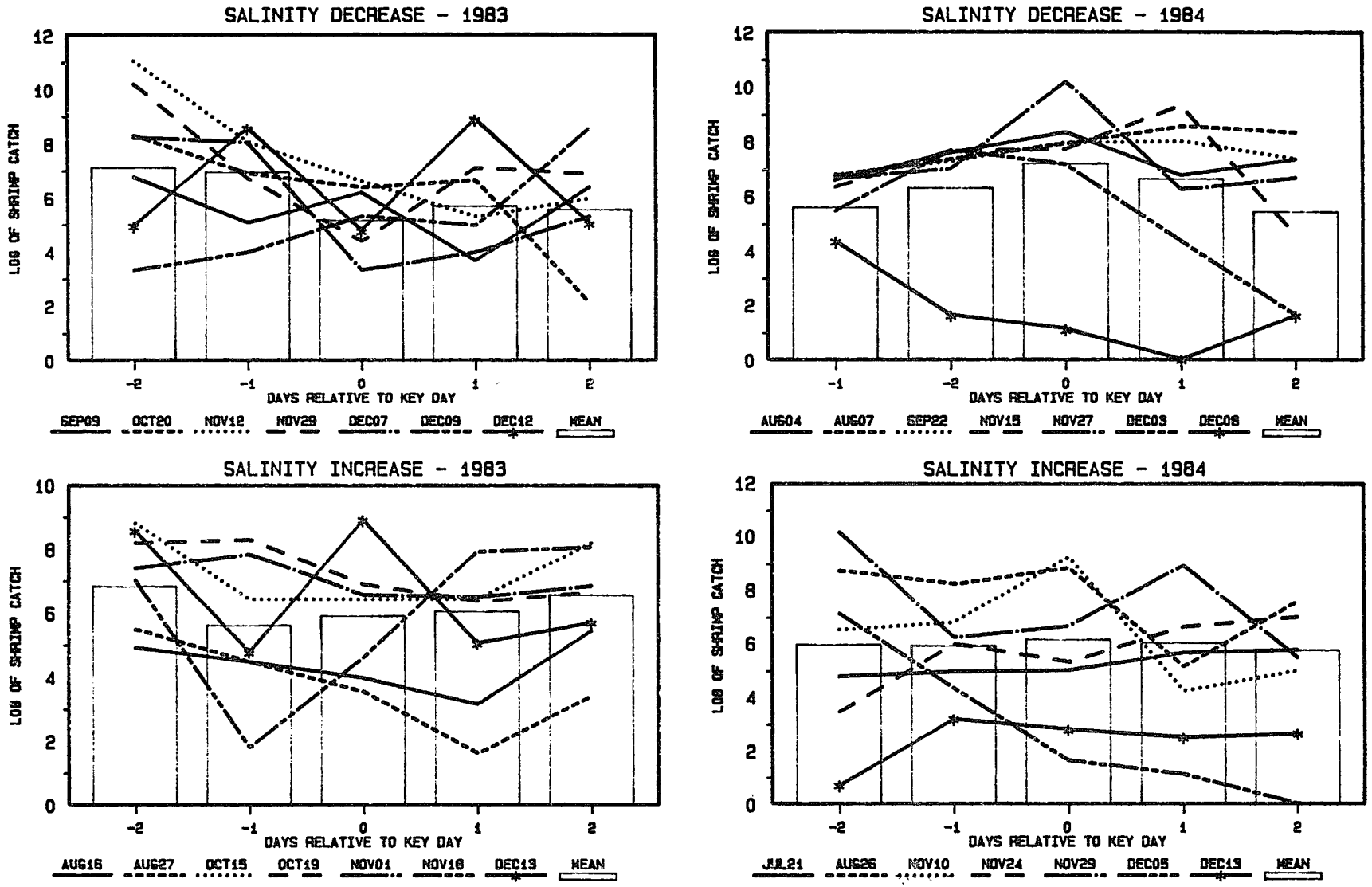


Figure 28. Natural log of white shrimp catch on days before, during, and after key salinity events.

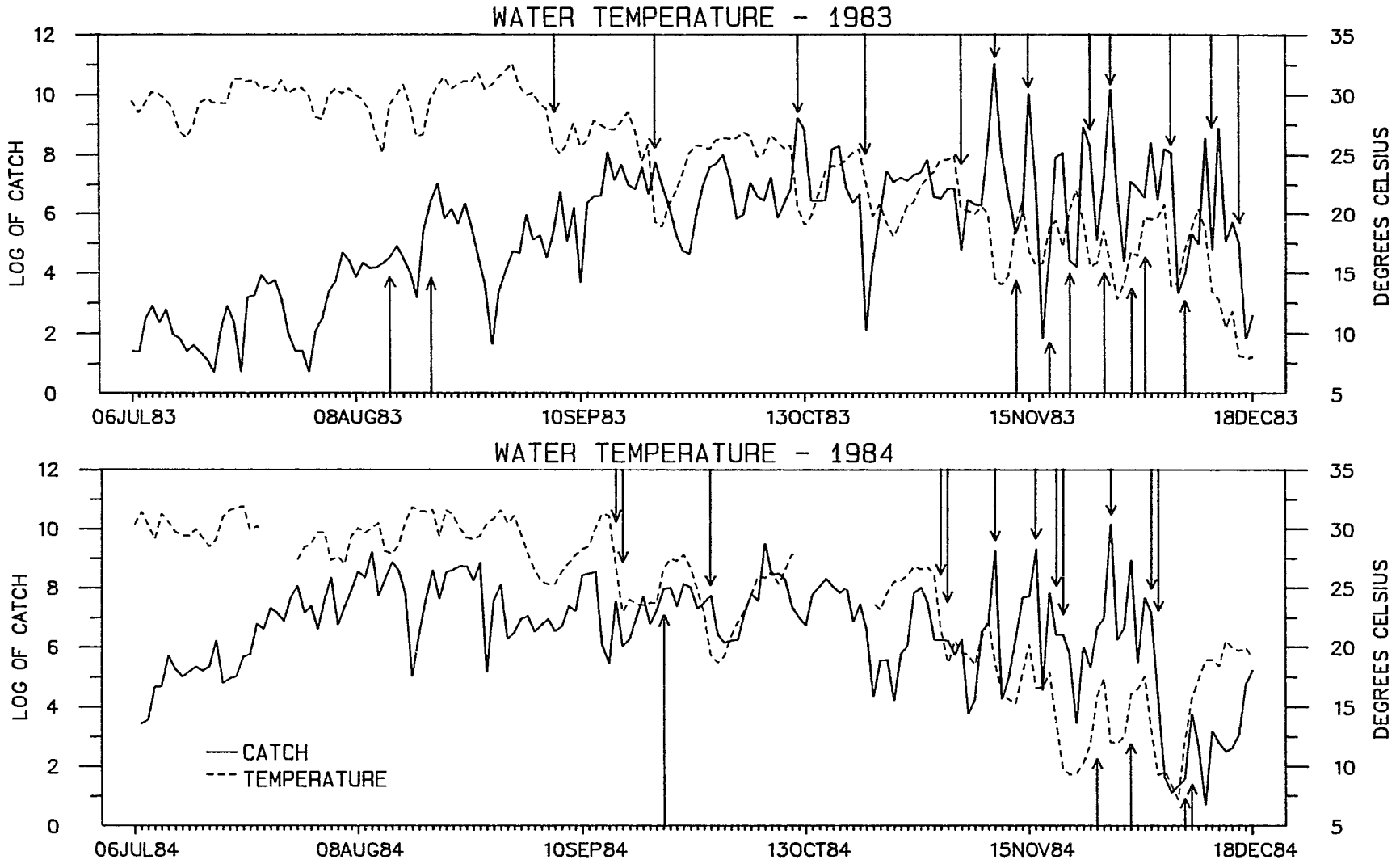


Figure 29. Natural log of white shrimp catch and water temperatures in 1983 and 1984. Arrows indicate key increases or decreases in temperatures.

day earlier, and other temperature variables, were negatively correlated with catch in summer, 1983, but this was due to a seasonal relation (Table 13, Figure 29). In fall, 1983, there was also a negative correlation but it was with change in minimum water temperature since the day before (Table 14); other temperature variables exhibited a positive relation (Table 14). This apparent contradiction was probably caused by 1) high values in catch coincident with low values in change in temperature (i.e., large decreases) since the day before, and vice versa) and 2) catch and temperature both following a general decreasing trend over the fall (Figure 29). No temperature variable was important in the 1983 stepwise regression.

In 1983 dramatic decreases in temperature were significantly related to higher than average catches, as determined by epoch analysis (Table 16, Figure 29). Dramatic increases in temperature were nearly significantly related to small catches of emigrating white shrimp (Table 16, Figure 29).

In 1984, there was a positive correlation between catch and maximum air temperature yesterday ($r = 0.40$), among other temperature variables (Table 12). Although there seemed to be some times when temperature and catch were positively related on a daily basis, most of the correlation is probably due to a seasonal relationship (Figure 29). Temperature was not correlated with catch in summer, 1984, but was positively correlated in fall (Tables 13 and 14) when there was both a seasonal and, at times, a short-term relation between temperature and catch (Figure 29). Although there was no correlation with change in temperature (Table 14), it contributed to the 1984

stepwise regression model (Table 15). This relation can be seen in Figure 29; catch was often high on days when temperature dropped, and vice versa.

In 1984 there was also a significant relation between dramatic decreases in temperature and peaks in emigration, as determined by epoch analysis (Table 16, Figure 29). Coincidentally, the few dramatic increases in temperature were nearly significantly related to peaks in emigration as well (Table 16, Figure 29). This is probably because not all peaks in emigration were explained by temperature decreases alone.

Volume of Inflow and Outflow.- Catch was inversely correlated with volume of daily inflow over the entire season ($r = -0.35$), during fall, 1983 ($r = -0.55$) and in fall, 1984 ($r= -0.34$) (Tables 12 and 14). Apparently, catches tended to be greater on days of little or no inflow (Figure 30). Volume of inflow appeared as an inverse factor in the 1983 stepwise regression model (Table 15). Epoch analysis indicated that catches were significantly larger on days when inflow was dramatically low in both 1983 and 1984 and significantly smaller on days of dramatically high inflow in 1983 (Table 16, Figure 30). Furthermore, when daily inflow increased dramatically since the day before, there was a pattern of smaller catches on those days than on surrounding days, significantly so in 1983 (Table 16, Figure 30).

As might be expected, the reverse was true for the relation between catch and volume of outflow. Only the fall, 1983 relation between catch and outflow was correlated ($r = -0.37$, Table 14). However, epoch analysis indicated significantly larger catches on days of highest outflow in both years and significantly smaller catches

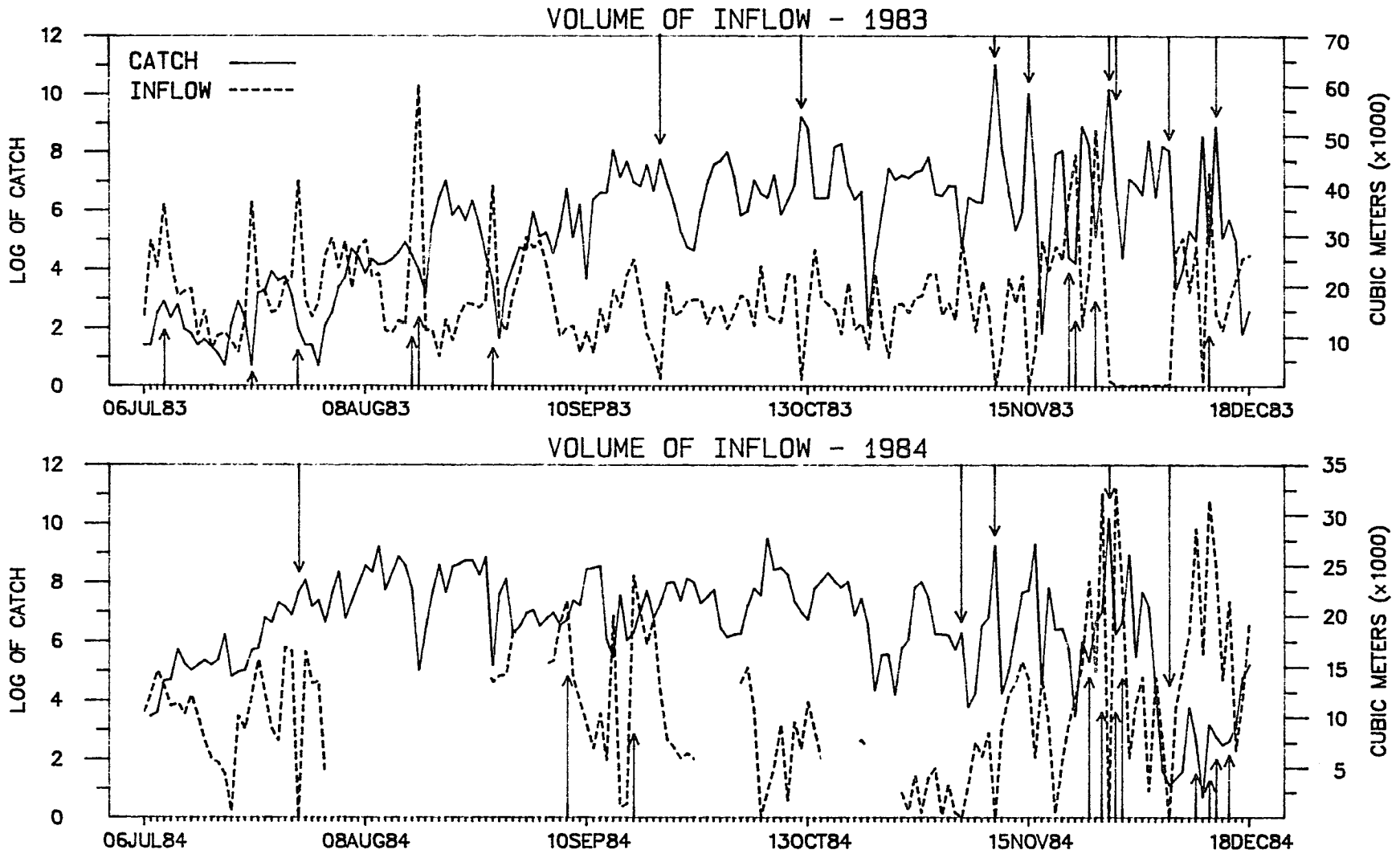


Figure 30. Natural log of white shrimp catch and inward flow in 1983 and 1984. Arrows indicate key days on which inward flow was lowest (down) or highest (up).

on days of dramatically low outflow in 1983 (Table 16, Figure 31). Furthermore, when daily outflow decreased dramatically since the day before in 1984, there was a significant pattern of smaller catches on those days than on surrounding days (Table 16, Figure 31).

Barometric Pressure.- Emigration of white shrimp, as reflected by daily catch, was weakly inversely correlated with the previous day's barometric pressure seasonally in 1984, when lagged 2 days in summer of 1983, and when lagged 1 day in fall of 1984 (Tables 12, 13, and 14, Figure 32). When barometric pressure is low catches are high, and vice versa. Barometric pressure did not appear in the stepwise regression models. Results from epoch analysis indicated that barometric pressure increasing since the day before was significantly related to catches higher than those on surrounding days in 1983 (Table 16, Figure 32). Larger catches also resulted from barometric pressure decreases 1 day prior to an observed catch; this relation was significant in 1983 and nearly so in 1984 (Table 16, Figure 32). The reverse was true when increasing barometric pressure 1 day prior to observed catches was analyzed; there were significantly smaller catches in 1984 and nearly significantly smaller catches in 1983 (Table 16, Figure 32).

Significantly smaller catches were observed on the days before the most dramatic decreases in barometric pressure in both years (Table 16, Figure 32). Significantly large catches were observed the day before dramatic increases in barometric pressure in 1983 but not in 1984 (Table 16, Figure 32). This phenomenon probably resulted from the cycling of fronts; the day before barometric pressure dropped substantially would have been a day of high pressure without much

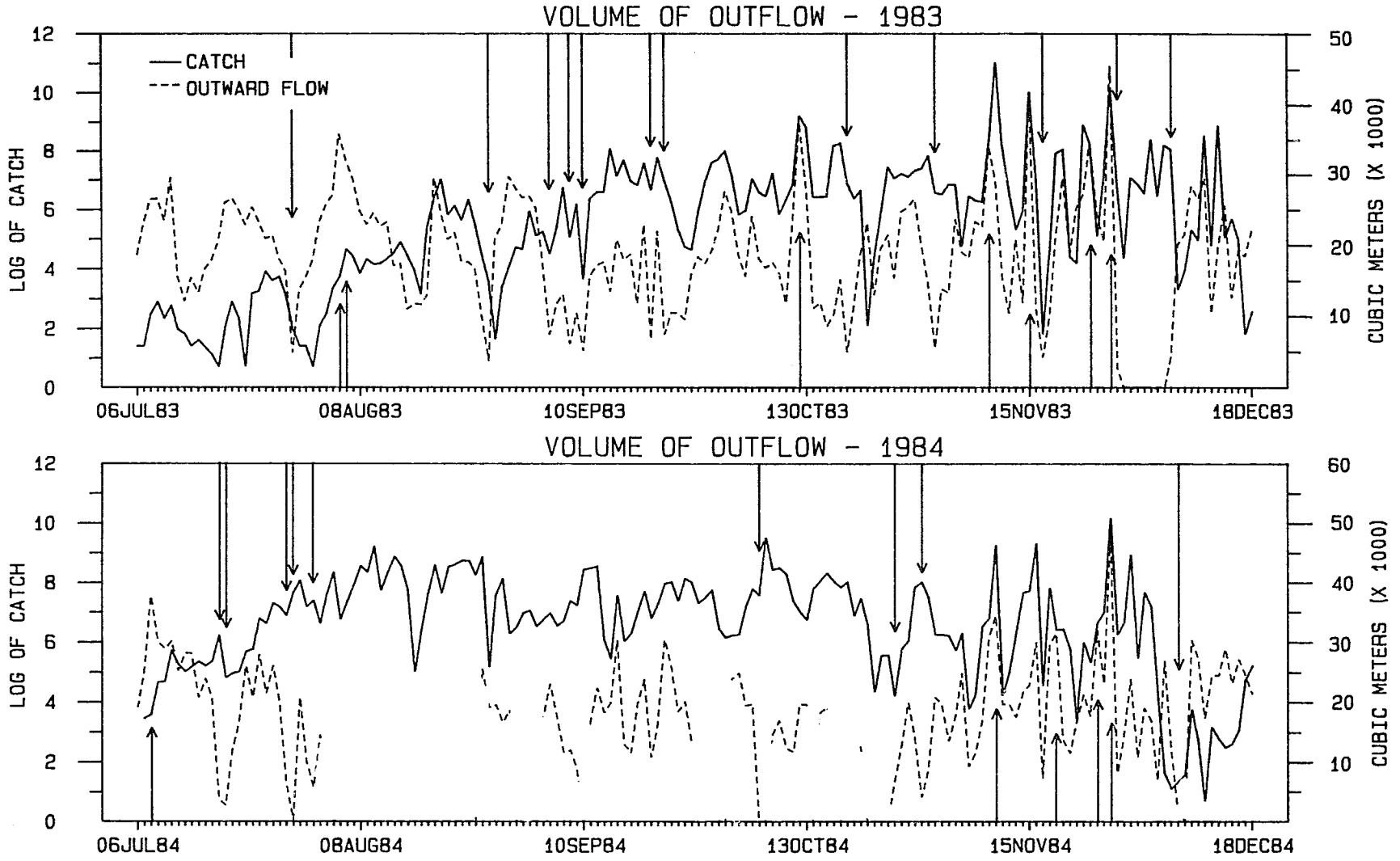


Figure 31. Natural log of white shrimp catch and outward flow in 1983 and 1984. Arrows indicate key days on which outward flow was lowest (down) or highest (up).

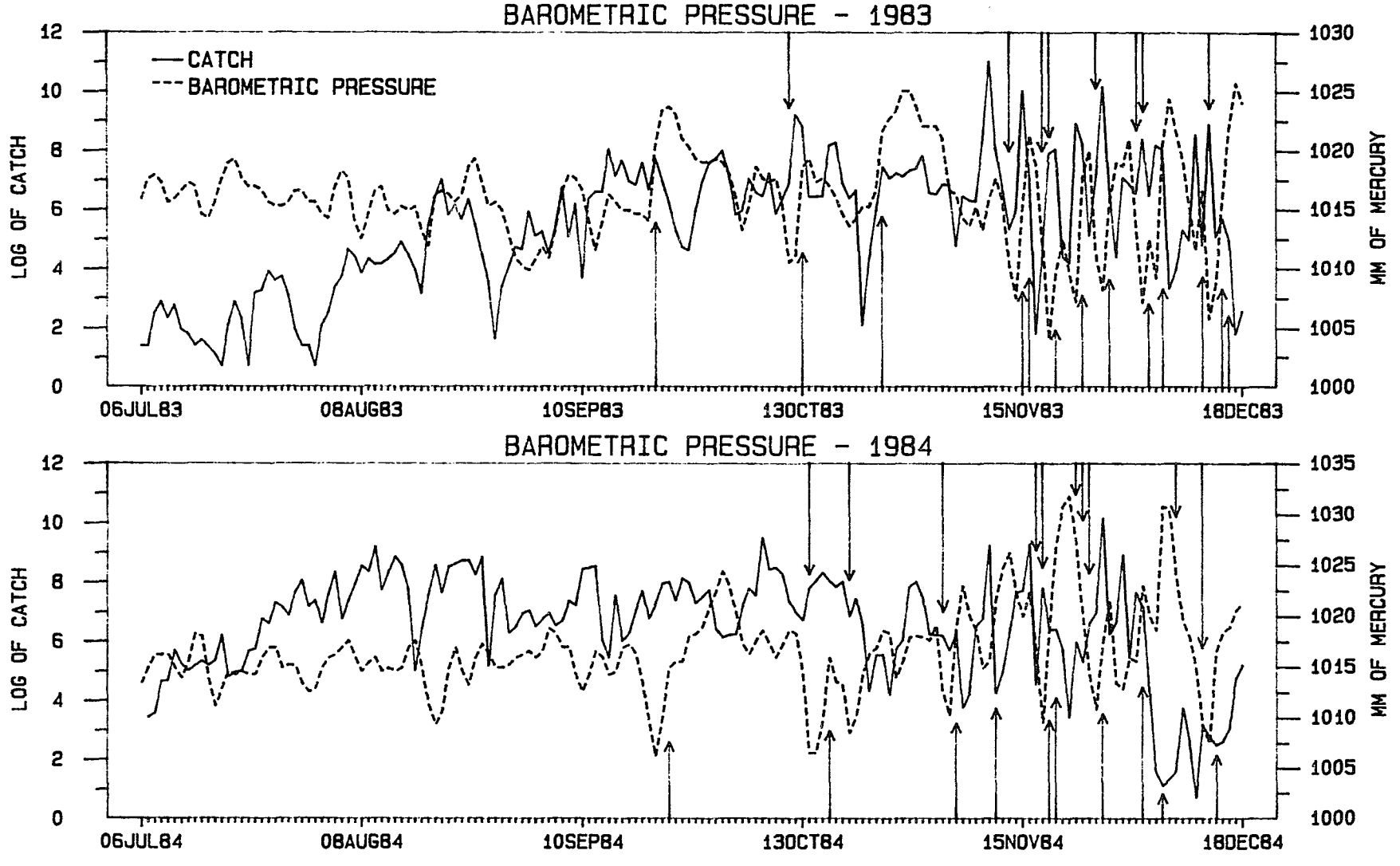


Figure 32. Natural log of white shrimp catch and barometric pressure in 1983 and 1984. Arrows indicate key days on which barometric pressure decreased (down) or increased (up) dramatically.

weather disturbance. This is verified by the results from the analysis of days having highest and lowest pressure. When pressure was lowest, catches were greater, significantly so in 1983 (Table 16, Figure 32). Catches were smaller on days having highest pressure but not significantly (Table 16).

Precipitation.- Precipitation did not appear in any linear modeling probably because of the large number of days with no rainfall. However, epoch analysis revealed a significant relation between rainfall and white shrimp emigration 1 day later in 1984 (Table 16, Figure 33). Although not significant, the same relation appeared to occur in 1983 (Figure 33). This could easily be related to increased outflow. Of the two variables, the driving mechanism, if there is one, remains unknown.

pH.- White shrimp emigration was positively correlated with pH variables over the entire 1983 season but was inversely correlated in 1984 (Table 12). This was likely due to a coincidental, seasonal, positive relation in 1983 and a seasonal inverse relation in 1984 (Figure 34). There was no correlation during summer (Table 13). There was no correlation between catch and pH in fall, 1983, but the two were inversely correlated in fall, 1984; pH was strongly correlated with catch ($r = -0.68$) (Table 14). The inverse relation may have been due to 1) a general trend downward in catch as fall progressed, while pH exhibited a slight, general upward trend, and/or 2) catch over several days was often low while pH was high (Figure 34). pH appeared in both stepwise models but probably for the same reasons cited above (Table 15). There was no response in catch due to dramatic pH

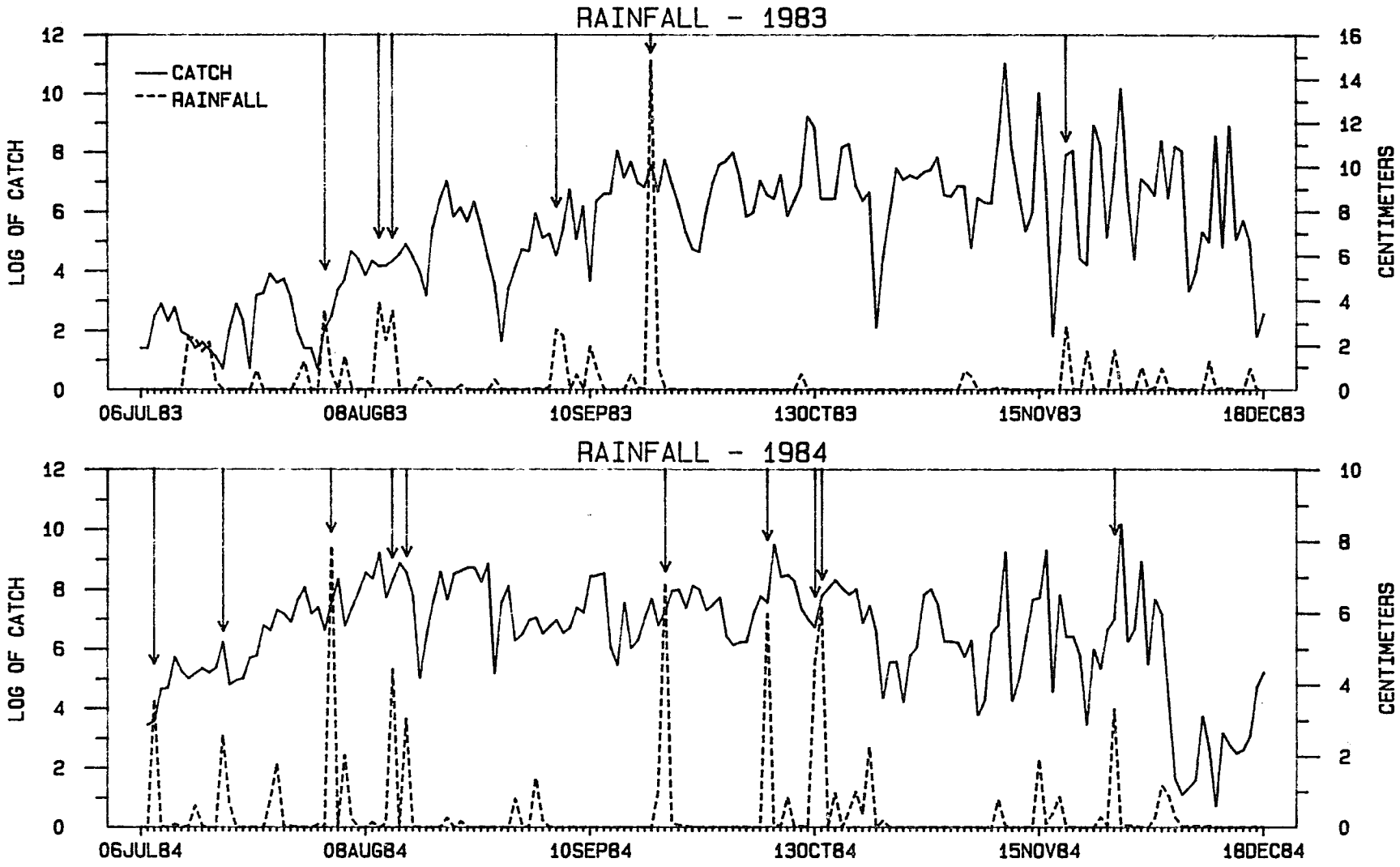


Figure 33. Natural log of white shrimp catch and rainfall in 1983 and 1984. Arrows indicate key days of rainfall.

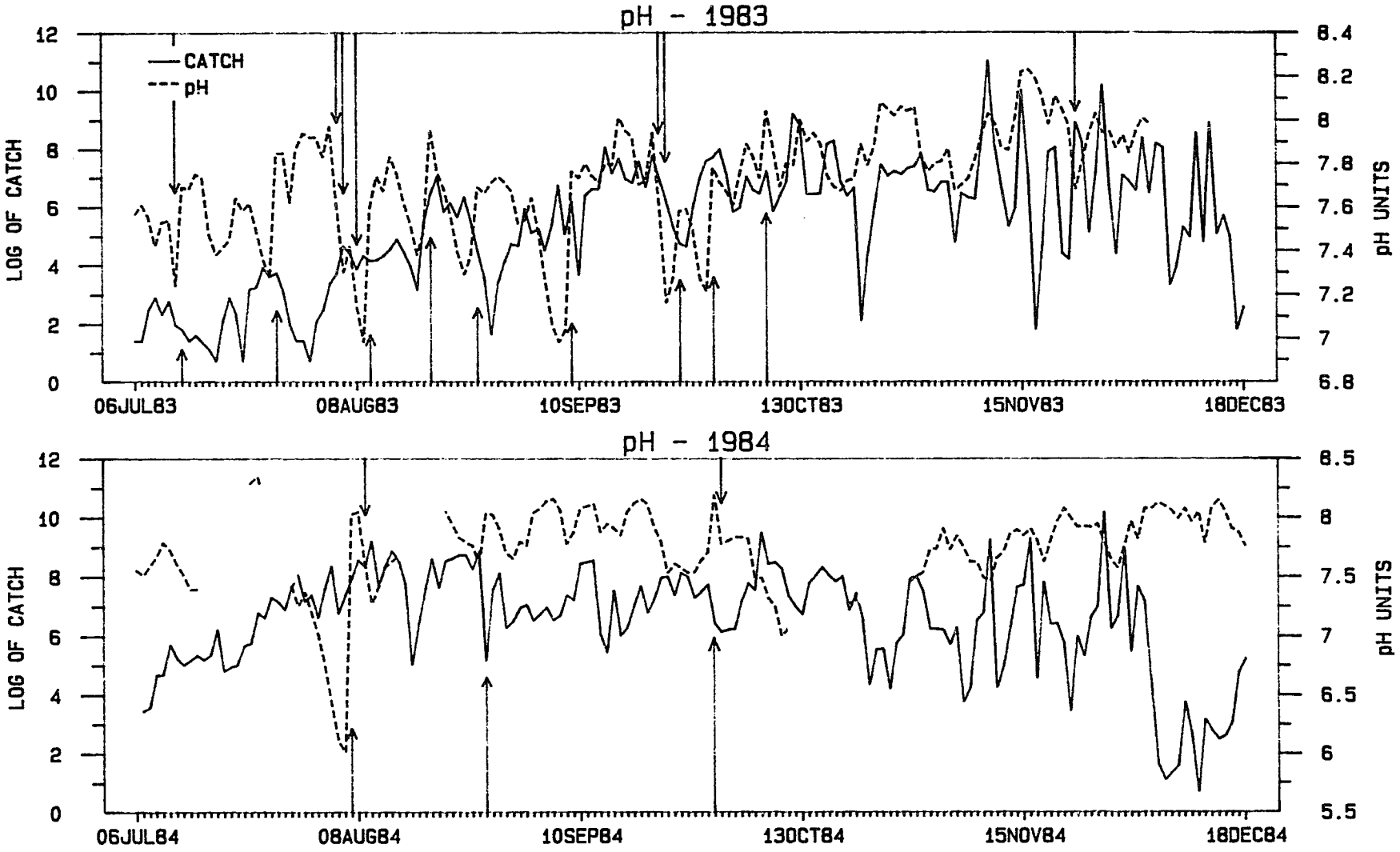


Figure 34. Natural log of white shrimp catch and pH in 1983 and 1984. Arrows indicate key days of pH increase (up) or decrease (down).

increases or decreases, according to epoch analysis.

The average pH value in 241 samples of rain collected in Lafayette in 1983-1984 was 5.21±0.67 (Braun 1984). The average pH during white shrimp presencein the study area was 7.72 in 1983 and 7.75 in 1984. There is a possibility that shrimp respond to decreases in pH resulting from rainfall. Again, although pH decreases could be stimulating emigration, decreasing barometric pressure, high outflow of water, and decreasing temperature all occur simultaneously with the decreasing pH and the responsibible variable, if there is one, is unknown.

Dissolved Oxygen.- Dissolved oxygen variables had a similar relation with white shrimp emigration as did pH (probably because pH and dissolved oxygen are related). Mean and maximum dissolved oxygen were positively correlated with catch over the entire season in 1983 but a number of dissolved oxygen variables were inversely correlated in 1984 (Table 12). There was no correlation between the two in summer (Table 13). During fall, 1983, catch was inversely correlated with mean and maximum dissolved oxygen of the previous day, apparently due to an actual daily inverse relation (Table 14, Figure 35). The variable "change in dissolved oxygen" was positively correlated with catch in fall, 1983; when dissolved oxygen decreased, catch decreased, and vice versa (although a high "change" value is positive, and a low "change" value is negative, in correlation "change" is still treated as a continuous variable centered around zero). This at first seems contradictory to the inverse relation between catch and dissolved oxygen noted above; however, because simultaneous decreases or increases in "change in dissolved oxygen" and catch results in a

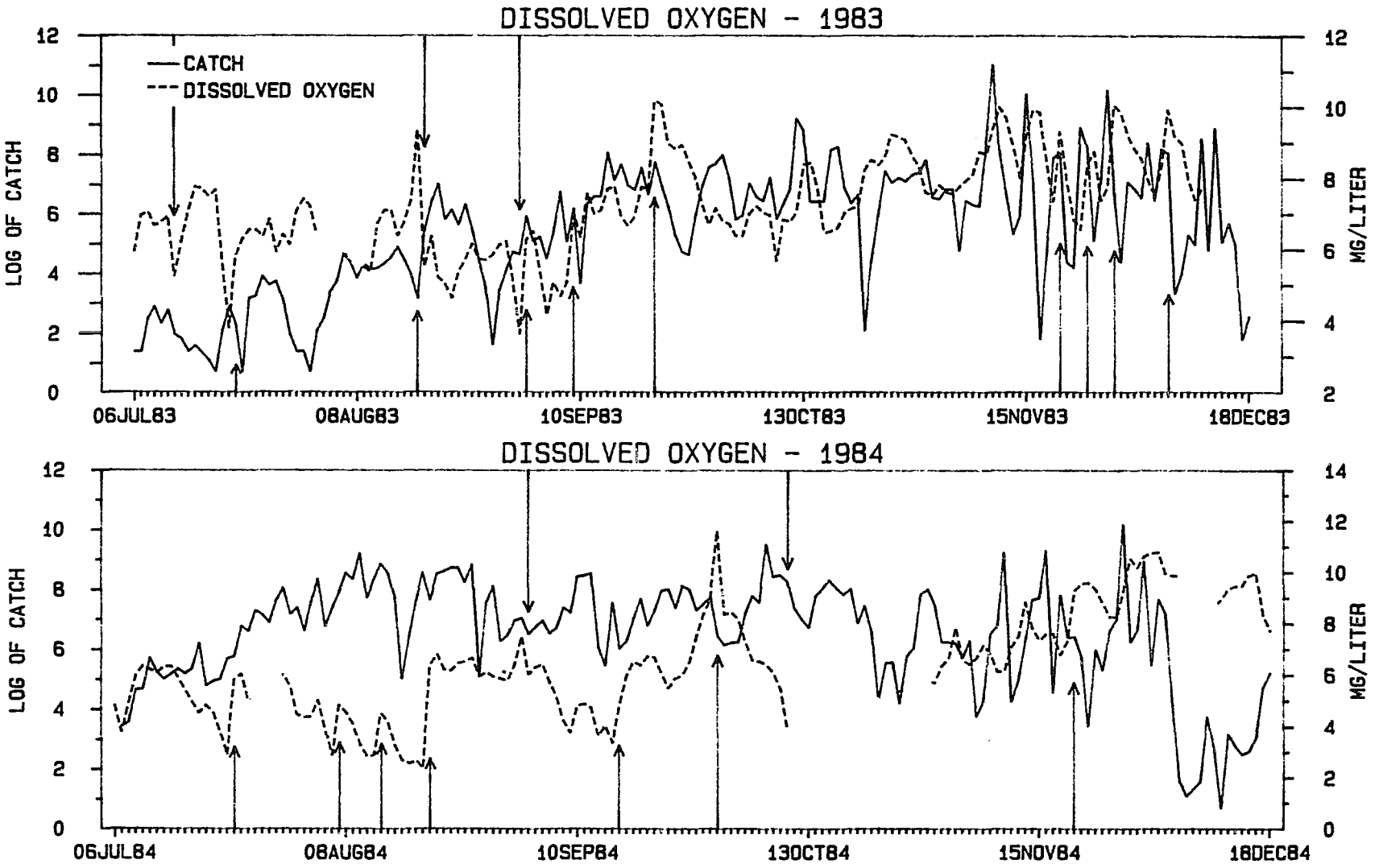


Figure 35. Natural log of white shrimp catch and dissolved oxygen in 1983and 1984. Arrows indicate key days of dissolved oxygen increase (up) or decrease (down).

positive relation, the absolute values of the variables can be opposite, resulting in an inverse relation (Figure 35). There was also an inverse relationship between dissolved oxygen variables and catch in fall, 1984 (Table 14, Figure 35). A dissolved oxygen variable appeared as an inverse factor in both stepwise regression models likely due to a combinationof seasonal and short-term relations as described for fall above (Table 15).

Greater catches may have occurred in response to an increase in dissolved oxygen in 1983 but not significantly, as determined by epoch analysis (Table 16, Figure 35). More importantly, catches were significantly greater on days preceding key days of both increasing and high dissolved oxygen in 1983 (Table 16, Figure 35). Larger catches may have also occurred on 1984 days preceding dramatic increases in dissolved oxygen but they were not significant (Table 16). I believe this may be a coincidental relationship: rainfall causes dissolved oxygen (and pH) to decrease while also increasing the likelihood of high outflow; by the time shrimp are emigrating in response to high outflow, dissolved oxygen begins rising, resulting in the relation of high catch on the day preceding high, or increasing, dissolved oxygen.

Length at emigration

No obvious relationships were discovered in graphs of environmental variables and mean length at emigration. Since sudden decreases in temperature have been implicated as stimulating large outward migrations, a graph for this particular variable only is presented. However, there seem to be no significant short-term events

relating temperature to mean length (Figure 36). There does appear to be a general relation between decreasing water temperature and decreasing length at emigration from about the first of November until the end of emigration in both years (Figure 36).

The relation between mean daily length and total number emigrating was contradictory in 1983 and 1984 (Figure 37). Although both slopes were significantly different fom 0, the regressions were very weak (1983 r^2 = 0.13, 1984 r^2 = 0.05). Assuming the number of shrimp emigrating indicates the magnitude of stimulation for emigration, a positive relation might imply stimulation occurs more for larger shrimp, or vice versa, but the relations were weak and contradictory (probably because the assumption was not met), so no such conclusions could be reached. A decrease in mean length when emigration peaked could indicate emigration in response to environmental stimuli is not strictly size-dependent. In some cases at least, mean length did decrease during peak emigrations (Figure 38).

There was a positive relation between coefficient of variation of daily lengths and total catch (Figure 39). Although the relations were weak (1983 r^2 = 0.06, 1984 r^2 = 0.07), both slopes were significant ($P < 0.01$). Thus, on days of large emigrations, there is a wider size range of emigrants, perhaps meaning that shrimp of a wider range of sizes respond to the stimulus to emigrate.

Early summer was not included in analyses of size trends over time because mean length was confounded by the presence of very large shrimp which had entered early in the spring. A second period, 10 August through 1 November, was chosen for analysis because it appeared

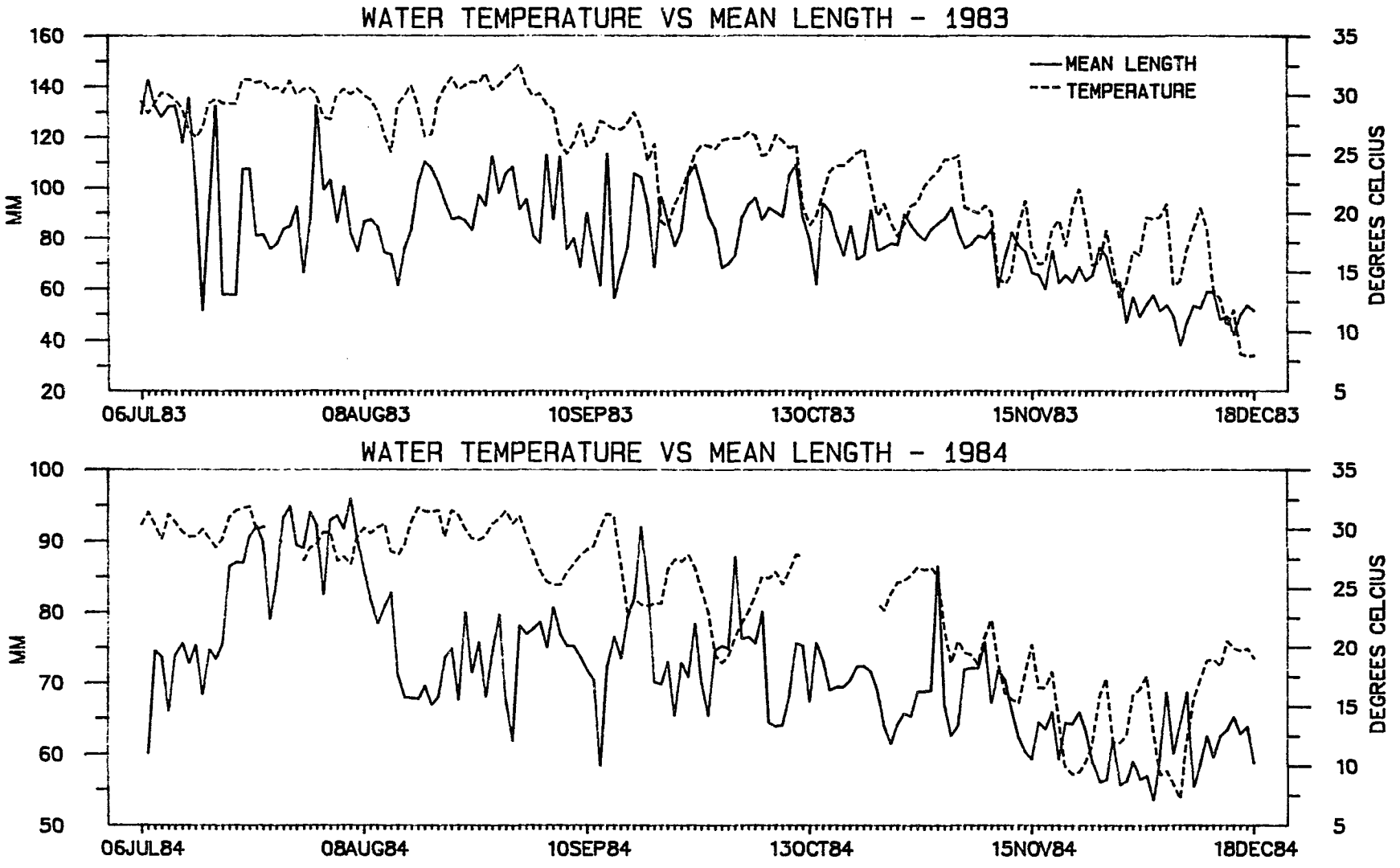
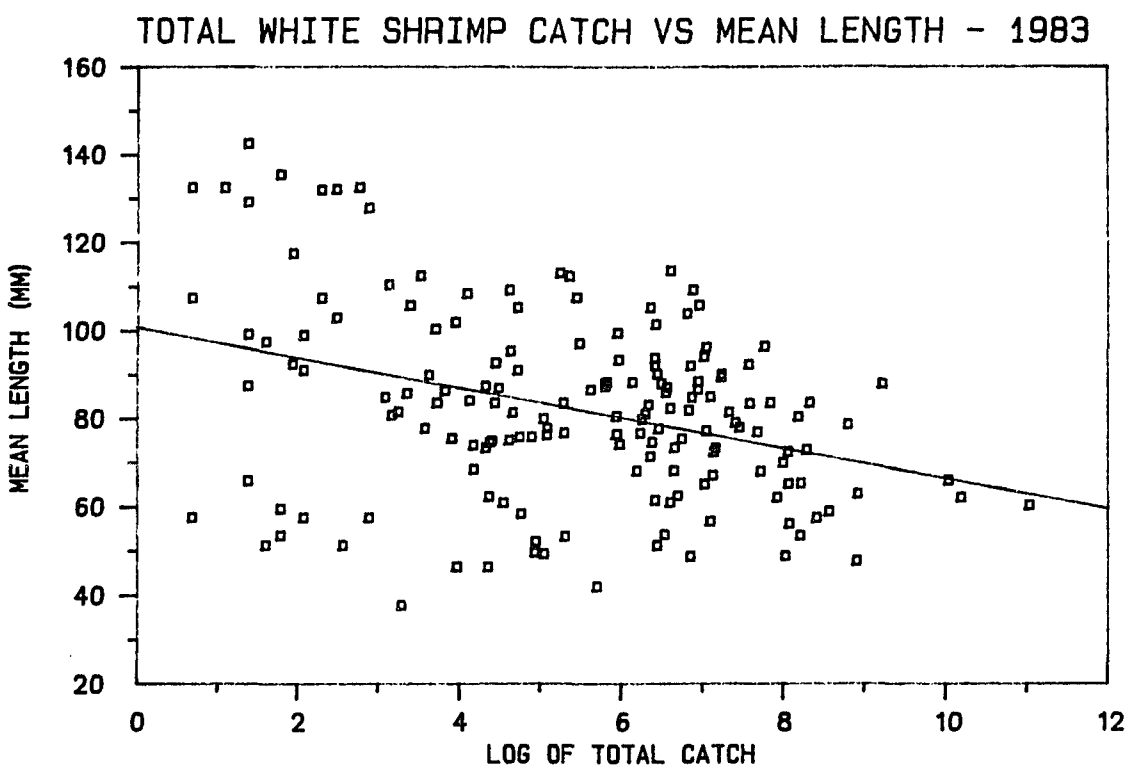


Figure 36. Daily mean lengths of emigrating white shrimp and water temperatures.



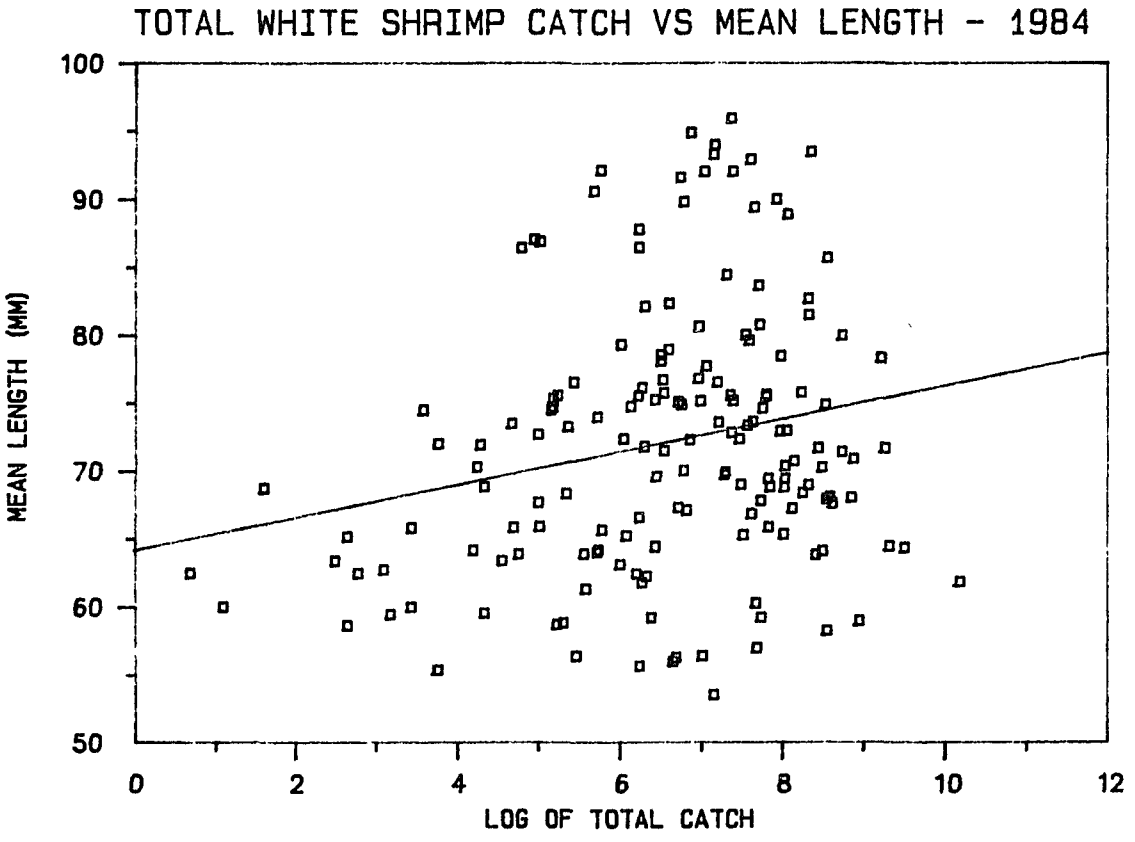


Figure 37. Relation between mean length and total catch of emigrating white shrimp.

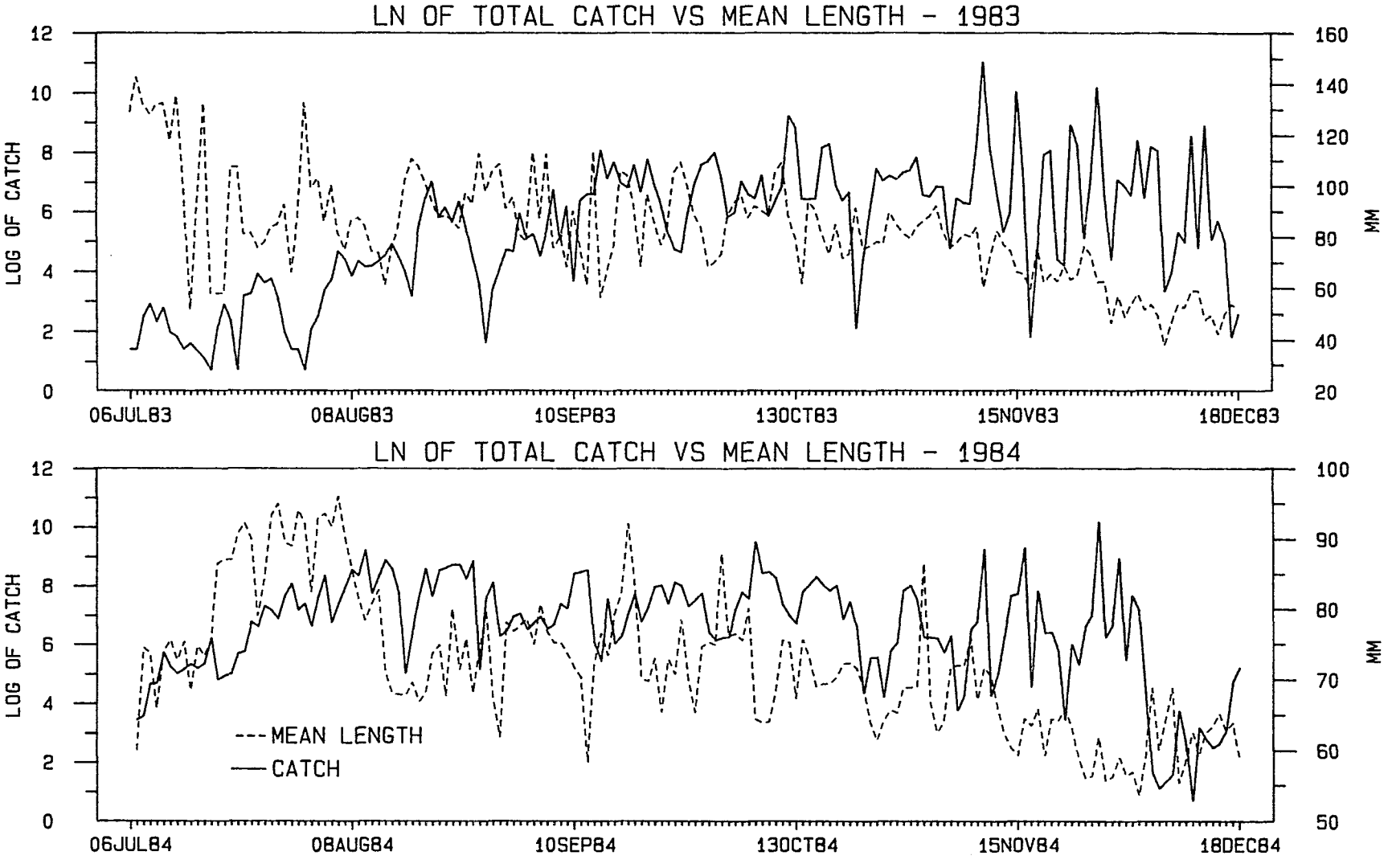
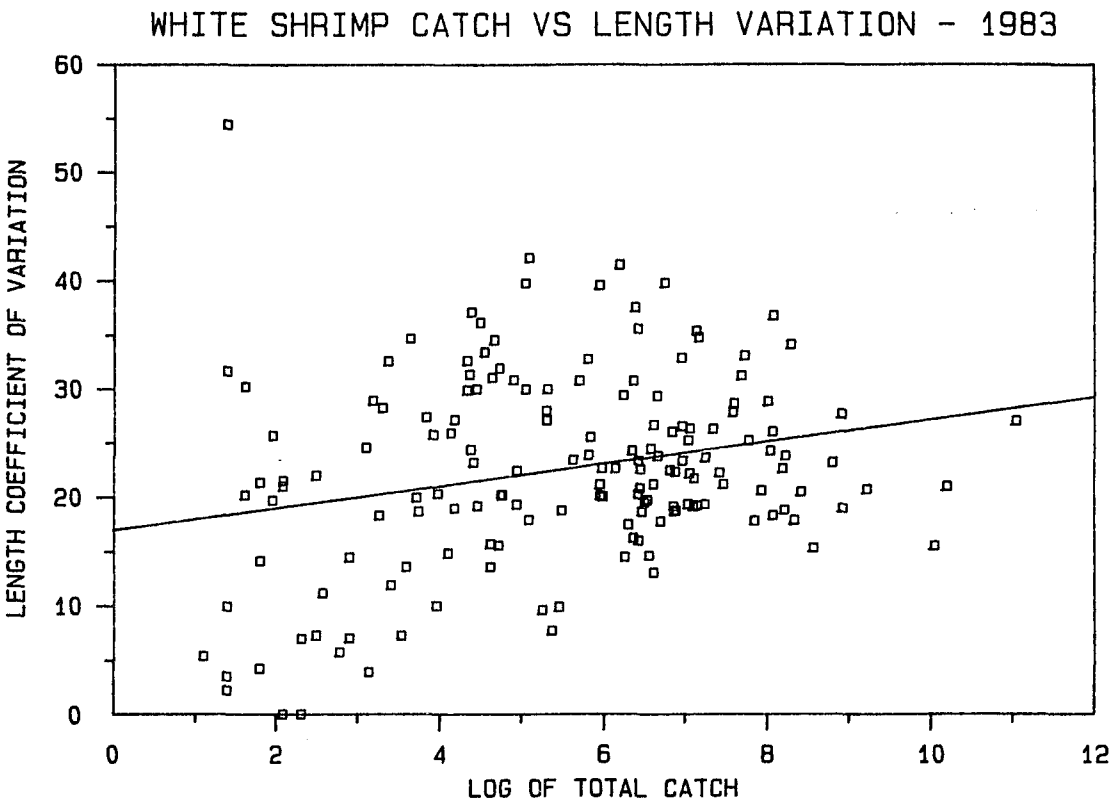


Figure 38. Daily log of white shrimp catch and mean lengths in 1983 and 1984.



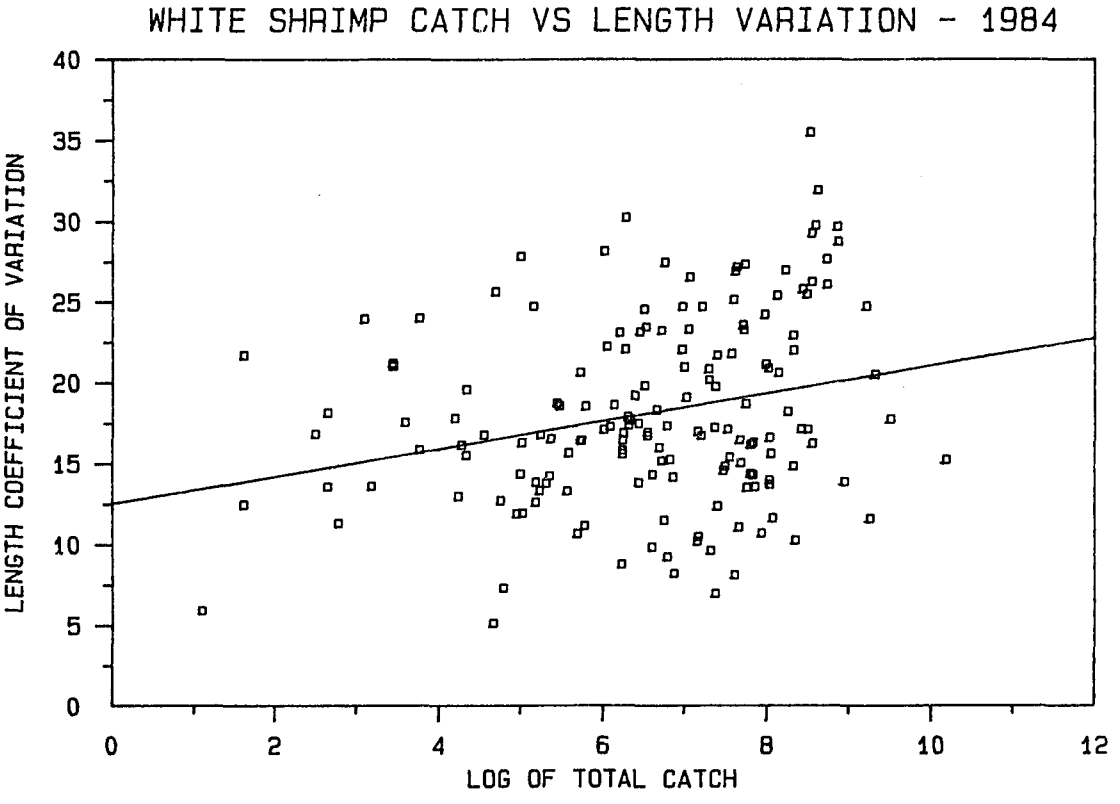


Figure 39. Relation between variation in length and total catch of white shrimp.

to potentially be a steady-state period for length at emigration (Figure 36). Length at emigration declined very gradually through this period. The relation was weak (1983 r^2 = 0.04, 1984 r^2 = 0.04) and the slopes only approached significance (1983 P = 0.0935, 1984 P = 0.0715). Since shrimp were growing during this period (Chapter IV), this weak trend of general decrease in size over the major emigration period validates the theory that white shrimp emigration from the marsh is a gradual "bleeding-off" of the larger individuals (Herke 1971).

The third period was the period of declining mean lengths, 1 November through 18 December (Figure 36). Length at emigration declined significantly ($P < 0.0001$ in both 1983 and 1984). The fit of these two models was quite good (1983 r^2 = 0.76, 1984 r^2 = 0.28). This phenomenon may result from increasing emigration response in smaller and smaller shrimp relative to the effects of declining temperature or day length as the fall progresses.

DISCUSSION

Examining relations between daily catches and observations of daily environmental variables is not easily amenable to any one analytical technique. None of the methods applied here could be used alone to explain emigration. Even with a combination of techniques, uncertainties remain regarding the mechanisms of environmental influence on emigration. This is probably because 1) change in a given variable does not always elicit the same response in shrimp, 2) the number of shrimp available to emigrate is influenced by time and the number which emigrated in the preceding days, 3) if emigration is

size-dependent, the number of shrimp that have attained the emigration size is variable, and 4) the environmental variables are not independent. Thus, results for each variable must be considered in concert with others and the number of shrimp available to emigrate (Table 17).

Linear models did not perform well for describing the short-term relationships between emigration and potential environmental cues. This was probably because linear models incorporate information about linear trends for the entire period being analyzed and discern short-term associations only when the variables cycle together. Superposed epoch analysis worked well to identify single events relating environmental cues to emigration, but only if the relationship was consistent from event to event.

Generally though, my results confirm what every Cajun shrimper already knows: that white shrimp emigrate from coastal marshes as autumn cold fronts pass. Previous researchers concluded sharp declines in water temperature were most influential in white shrimp emigration (Lindner and Anderson 1956; Gaidry and White 1973; Rogers and Herke 1985b) but no one has documented the effect of other variables associated with cold fronts such as barometric pressure, rainfall, decreasing salinity, and dramatic outflow of water. While it remains unclear which particular variable is the driving force for emigration, it is clear that outward flow, decreasing or low barometric pressure and perhaps rainfall, as well as decreasing temperature, may be important factors affecting emigration (Table 17). These variables may synergistically or singly influence emigration. Further, a given

Table 17. Summary of environmental variables apparently affecting white shrimp emigration, by analytical approach (G = graphic, C = correlation, R = multiple regression, and E = epoch analysis).

	Large catch		Small catch	
Effect	Variable high or increasing	Variable low or decreasing	Variable high or increasing	Variable low or decreasing
Salinity		G	G	
Temperature		GCRE	GCR	
Volume of inflow		GCRE	GCRE	
Volume of outflow	GE	C	C	GE
Barometric pressure		GCE	GCE	
Precipitation	E			
pH		GCR	GCR	
Dissolved oxygen	GE	CR	CR	

variable could be most important under certain conditions while another variable is more important under other conditions. Since emigration occurs continuously, but is highly variable from day to day, perhaps some variable(s) are more important than others in stimulating emigration. However, because emigration is continuous, it is also likely that there are several influential variables, some being more influential than others. Of course, although this chapter is focused on external emigration cues, much of the drive to emigrate may be endogenous. There is likely some degree of interaction of internal and external cues and these may vary with shrimp size/age and environmental variable intensity.

Although catches were significantly greater on days of dramatic salinity decrease in 1984, the reverse was true in 1983. The inverse relation between summer riverine discharge and shrimp abundance observed on a coastwide basis (Barrett and Gillespie 1973) is probably not due to salinity, per se, limiting shrimp production in coastal marshes. This study indicates that white shrimp may be tolerant of dramatic, short-term salinity changes, as indicated by previous laboratory studies on white shrimp and salinity (Zein-Eldin 1963). Furthermore, white shrimp were abundant in salinities of 1.33-24.58 ppt in 1983 and 4.16-21.59 ppt in 1984 without large emigrations when salinity approached those extremes. Apparently, seasonal variations in white shrimp production are directly related to freshwater outflow, rather than salinity itself. This is probably due to the inability of shrimp to move marshward during periods of higher freshwater discharge. Because shrimp are transported by tidal currents into the marsh, periods of high rainfall cause water to flow outward more, to

the detriment of shrimp.

Dissolved oxygen may play an important role in white shrimp emigration. Both correlation and superposed epoch analyses indicated an inverse relation between dissolved oxygen and catch. While the mechanisms of the relation remain unknown, some possible explanations include 1) the lagged emigration of shrimp in response to low dissolved oxygen, 2) coincidental relation due to increasing dissolved oxygen following passage of weather fronts, 3) increases in dissolved oxygen following mass emigrations of shrimp in response to other variables, or 4) a combination of the foregoing factors.

It was not possible to conclusively find a relation between length at emigration and potential environmental stimuli. This is probably because, if there is a relation, it may be subtle and/or hidden in the extreme day to day variation in catches. While Herke's (1971) hypothesis that emigration is in response to environmental cues and increase in size could not be conclusively validated, his concept of white shrimp emigration occurring as a "bleeding-off" of larger individuals was substantiated.

Based on the foregoing, and the fact that most white shrimp movement occurs at night (Herke et al. 1987b), I would presently recommend that marsh managers open water control structures for emigrating white shrimp when cold fronts pass during September-December, at least at night. Of course, opening structures to let shrimp out will only be useful if they have been let in; this points up the need for detailed research on the conditions which enhance white shrimp access to the marsh.

Conclusions

1. There was no clear effect of salinity on white shrimp emigration.
2. Peak catches of emigrating white shrimp are often related to temperature decreases.
3. White shrimp emigration was clearly positively affected by flow from the marsh.
4. Barometric pressure appeared to have a strong influence on white shrimp emigration; decreasing and/or low barometric pressure was often followed by large catches of emigrants.
5. Rainfall may trigger emigration but the association between rainfall and emigration may actually be due to the relation between rainfall and barometric pressure or outward water flow.
6. There was no obvious relation between pH and white shrimp emigration.
7. Dissolved oxygen was often high the day after large catches occurred. This could have been due to a relation between weather phenomena and dissolved oxygen such as the aeration caused by rainfall and wind or the production of oxygen by aquatic plants on a sunny, high pressure day.
8. Generally, weather resulting from cold fronts apparently causes those white shrimp ready to emigrate to leave the marsh in fall.
9. A regression-based predictive model could not be developed.

10. No relation could be found between length at emigration and environmental variables.
11. White shrimp emigration through the fall is a "bleeding-off" of the larger individuals although no relation between that larger size and any particular environmental stimuli could be discovered.
12. It is recommended that marsh managers open water control structures (especially at night) to allow white shrimp to emigrate when a front is predicted to pass anytime from early September to the end of December.
13. Linear models did not describe short-term relationships between environmental variables and emigration well. Superposed epoch analysis was much better for this purpose.

REFERENCES

Adkins, G., and P. Bowman. 1976. A study of the fauna in dredged canals of coastal Louisiana. Technical Bulletin 18, Louisiana Wildlife and Fisheries Commission, New Orleans.

Barrett, B. B., and M. C. Gillespie. 1973. Primary factors which influence commercial shrimp production in coastal Louisiana. Louisiana Wildlife and Fisheries Commission Technical Bulletin Number 9, Baton Rouge.

Baumann, R. H., and R. D. DeLaune. 1982. Sedimentation and apparent sea-level rise as factors affecting land loss in coastal Louisiana. Pages 2-13 *in* D. F. Boesch, editor. Proceedings of the Conference on Coastal Erosion and Wetland Modification in Louisiana: Causes, Consequences, and Options. U. S. Fish and Wildlife Service, National Coastal Ecosystem Team. FWS/OBS-82/59.

Boesch, D. F., J. W. Day, and R. E. Turner. 1984. Deterioration of coastal environments in the Mississippi deltaic plain: options for management. Pages 447-466 *in* V.S. Kennedy, editor. The estuary as a filter. Academic Press, Orlando, Florida.

Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460-468.

Bradshaw, W. H., 1985. Relative abundance of small brown shrimp as influenced by semi-impoundment. Master's Thesis. Louisiana State University, Baton Rouge.

Braun, R. D. 1984. A study of the pH of rain in Lafayette, Louisiana. Proceedings of the Louisiana Academy of Sciences 48:42-44.

Chabreck, R.H. 1968. Weirs, plugs and artificial potholes for the management of wildlife in coastal marshes. Pages 178-192 *in* J.D. Newsom, editor. Proceedings of the Marsh and Estuary Management Symposium. Division of Continuing Education, Louisiana State University, Baton Rouge.

Chabreck, R. H., and R. G. Linscombe. 1982. Changes in vegetative types in Louisiana coastal marshes over a 10-year period. 45:98-102.

Chen, X. Z., W. H. Herke, E. E. Knudsen, B. D. Rogers, and G. P. Shaffer. 1987. Entropy data analysis as a parameter-free modeling technique. Pages 1687-1693 *in* M. Willumsen, R. D. Cruz, W. G. Vogt, and M. H. Mickle, editors. Modeling and simulation: Proceedings of the eighteenth annual Pittsburgh Conference. Instrument Society of America, Research Triangle Park, North Carolina.

Clark, S. H., and C. W. Caillouett, Jr. 1973. White shrimp (*Penaeus setiferus*) population trends in a tidal marsh pond. Marine Fisheries Review 35:27-29.

Condrey, R. E., J. G. Gosselink, and H. J. Bennett. 1972. Comparison of the assimilation of different diets by *Penaeus setiferus* and *P. aztecus*. Fishery Bulletin 70:1281-1292.

Copeland, B. J. 1965. Fauna of the Aransas Pass Inlet, Texas. I. Emigration as shown by tide trap collections. Publications of the Institute of Marine Science, University of Texas 10:9-21.

Cowan, J. H., Jr., R. E. Turner, and D. R. Cahoon. 1988. Marsh management plans in practice: Do they work in coastal Louisiana, USA Environmental Management 12:37-53.

Freund, R. J., and R. C. Littel. 1981. SAS for linear models, a guide to the ANOVA and GLM procedures. SAS Series in Statistical Applications, SAS Institute, Cary, North Carolina.

Gaidry, W. J., III, and C. J. White. 1973. Investigations of commercially important penaeid shrimp in Louisiana estuaries. Louisiana Wildlife and Fisheries Commission, Technical Bulletin 8.

Gosselink, J. G. 1984. The ecology of delta marshes of coastal Louisiana: a community profile. U.S. Fish and Wildlife Service, FWS/OBS-84/09.

Guillory, V. J., J. E. Roussel, and C. Miller. 1981. Appraisal of otter trawl tow lengths and replicate sampling. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 34:158-166.

Gulland, J. H. 1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Manuals in Fisheries Science, Number 4.

Herke, W. H. 1968. Weirs, potholes and fishery management. Pages 193-211 *in* J.D. Newsom, editor. Proceedings of the Marsh and Estuary Management Symposium. Division of Continuing Education, Louisiana State University, Baton Rouge.

Herke, W. H. 1969. A boat-mounted surface push-trawl for sampling juveniles in tidal marshes. Progressive Fish Culturist 31: 177-179.

Herke, W.H. 1971. Use of natural, and semi-impounded, Louisiana tidal marshes as nurseries for fishes and crustaceans. Doctoral dissertation. Louisiana State University, Baton Rouge.

Herke, W.H. 1977. Life history concepts of motile estuarine-dependent species should be re-evaluated. W. H. Herke, 555 Staring Lane, Baton Rouge, Louisiana.

Herke, W. H. 1978. Subsampler for estimating the number and length frequency of small, preserved nektonic organisms. Fishery Bulletin 76:490-494.

Herke, W. H. 1979. Some effects of semi-impoundment on coastal Louisiana fish and crustacean nursery usage. Pages 325-346 *in* J.W. Day, D. D. Culley, Jr., R. E. Turner, and A. J. Mumphrey, Jr., editors. Proceedings of the Third Coastal Marsh and Estuarine Management Symposium. Division of Continuing Education, Louisiana State University, Baton Rouge.

Herke, W. H., B. D. Rogers, and J. A. Grimes. 1984a. A study of the seasonal presence, relative abundance, movements, and use of habitat types by estuarine-dependent fishes and commercially important decapod crustaceans on the Sabine National Wildllife Refuge. Final Report for Cooperative Agreement FWS Number 14-16-0009--79-1003. Louisiana Cooperative Fishery Research Unit, Louisiana State University Agricultural Center, Baton Rouge.

Herke, W. H., B. D. Rogers, and E. E. Knudsen. 1984b. Habits and habitats of young spotted seatrout in Louisiana marshes. School of Forestry, Wildlife and Fisheries. Research Report Number 3.

Herke, W. H., E. E. Knudsen, P. A. Knudsen, and B. D. Rogers. 1987a. Effects of semi-impoundment on fish and crustaceans nursery use: evaluation of a "solution". Pages 2562-2576 *in* O. T. Magoon, H. Converse, D. Minor, L. T. Tobin, D. Clark, and G. Domurat editors. Coastal Zone '87. American Society of Civil Engineers, New York.

Herke, W. H., E. E. Knudsen, X. Z. Chen, N. S. Greene, P. A. Knudsen, and B. D. Rogers. 1987b. Final report for the Cameron-Creole Watershed Fisheries Investigations. Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge.

Herke, W. H., M. W. Wengert, and M. L. LaGory. 1987c. Abundance of young brown shrimp in natural and semi-impounded marsh nursery areas: relation to temperature and salinity. Northeast Gulf Science 9:9-28.

Holden, M. J., and D. F. S. Raitt. 1974. Manual of fisheries science. Part 2, Methods of resource investigations and their application. FAO Fisheries Technical Paper Number 115. Food and Agricultural Organization of the United Nations, Rome, Italy.

King, B. D., III. 1971. Study of migratory patterns of fish and shellfish through a natural pass. Texas Parks and Wildlife Department Technical Series Number 9.

Klima, E. F. 1965. Evaluation of biological stains, inks, and fluorescent pigments as marks for shrimp. U.S. Fish Wildlife Service Special Scientific Report Fisheries Number 511.

Klima, E. F. 1974. A white shrimp mark-recapture study. Transactions of the American Fisheries Society 103:107-113.

Knudsen, E. E., W. H. Herke, and J. M. Mackler. 1977. The growth rate of marked juvenile brown shrimp, *Penaeus aztecus*, in a semi-impounded Louisiana coastal marsh. Proceedings of the Gulf and Caribbean Fisheries Institute 29:144-159.

Knudsen, E. E., R. P. Paille, B. D. Rogers, W. H. Herke, and J. P. Geaghan. 1989. Effects of a fixed-crest water-control structure on brown shrimp growth rates, emigration patterns, and mortality rates in a shallow-water marsh nursery. North American Journal of Fisheries Management 9:411-419.

Knudsen, P. A. 1986. Emigration patterns and size characteristics of brown shrimp leaving a Louisiana coastal marsh. Master's Thesis. Louisiana State University, Baton Rouge.

Knudsen, P. A., W. H. Herke, and E. E. Knudsen. 1985. Emigration of brown shrimp from a low-salinity shallow-water marsh. Proceedings of the Louisiana Academy of Sciences 48:30-40.

Kutkuhn, J. H. 1966. The role of estuaries in the development and perpetuation of commercial shrimp resources. Pages 16-36 *in* R. F. Smith, A. H. Swartz, and W. H. Massman, editors. A symposium on estuarine fisheries. American Fisheries Society Special Publication Number 3.

Lindner, M. J., and W. W. Anderson. 1956. Growth, migrations, spawning, and size distribution of shrimp *Penaeus setiferus*. U. S. Fish and Wildlife Service, Fisheries Bulletin 56:553-645.

Loesch, H., J. Bishop, A. Crowe, R. Kuckyr, and P. Wagner. 1976. Technique for estimating trawl efficiency in catching brown shrimp (*Penaeus aztecus*), Atlantic croaker (*Micropogon undulatus*), and spot (*Leiostomus xanthurus*). Gulf Research Reports 5:29-33.

Minello, T. J., R. J. Zimmerman, and E. X. Martinez. 1987. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: effects of turbidity and substratum on predation rates. Fishery Bulletin 85:59-70.

Minello, T. J., R. J. Zimmerman, and E. X. Martinez. 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Transactions of the American Fisheries Society 118:693-708.

Nichols, S. 1984. Updated assessment of brown, white and pink shrimp in the U. S. Gulf of Mexico. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service. Unpublished manuscript presented to the 1985 Stock Assessment Workshop SAW/84/SHR/2.

Odum, E. P. 1984. The mesocosm. Bioscience 34(9): 558-562.

Parker, J. C. 1970. Distribution of juvenile brown shrimp (*Penaeus aztecus* Ives) in Galveston Bay, Texas, as related to certain hydrographic features and salinity. Contributions in Marine Science 15:1-12.

Parrack, M. L. 1981. Some aspects of brown shrimp exploitation in the northern Gulf of Mexico. Paper presented at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp, Key West, Florida (unpublished manuscript).

Perry, W. G. 1981. Seasonal abundance and distribution of brown and white shrimp in a semi-impounded Louisiana coastal marsh. Proceedings of the Louisiana Academy of Sciences 44:102-111.

Perry, W. G., and T. Joanen. 1986. Seasonal abundance and distribution of marine organisms in a semi-impounded Louisiana wildlife management area. Proceedings of the Louisiana Academy of Sciences 49:34-44.

Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. Canadian Journal of Fisheries and Aquatic Science 47:2-15.

Phares, P. L. 1980. Temperature associated growth of white shrimp in Louisiana. NOAA Tech. Mem. NMFS-SEFC-56. 19p.

Powers, J. E. 1984. Report of the second Southeast Fisheries Center stock assessment workshop, June 4-8, 1984. National Marine Fisheries Service, Miami, Florida.

Prager, M. H., and J. M. Hoenig. 1990. Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. Transactions of the American Fisheries Society 118:608-618.

Renfro, W. C. 1963. Small beam net for sampling postlarval shrimp. U.S. Bureau of Commercial Fisheries, Galveston, Texas. Circular 161:86-87.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.

Rogers, B. D., and W. H. Herke. 1985a. Estuarine-dependent fish and crustacean movements and weir management. Pages 210-219 *in* C. F. Bryan, P. J. Zwank, and R. H. Chabreck, editors. Proceedings of the Fourth Coastal Marsh and Estuary Management Symposium, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University Agricultural Center, Baton Rouge.

Rogers, B. D., and W. H. Herke. 1985b. Temporal patterns and size characteristics of migrating juvenile fishes and crustaceans in a Louisiana marsh. School of Forestry, Wildlife, and Fisheries, Research Report Number 5. Louisiana State University Agricultural Center, Baton Rouge.

Rogers, B. D., W. H. Herke, and E. E. Knudsen. 1987. Investigation of a weir-design alternative for coastal fisheries benefits. Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University Agricultural Center, Baton Rouge.

Rose, C.D., A.H. Harris, and B. Wilson. 1975. Extensive culture of penaeid shrimp in Louisiana salt-marsh impoundments. Transactions of the American Fisheries Society 104:296-307.

SAS Institute. 1988a. SAS/STAT User's Guide. Release 6.03 edition. Cary, North Carolina.

SAS Institute. 1988b. SAS Procedure Guide, Release 6.03 edition. Cary, North Carolina.

SAS Institute. 1988c. SAS Language Guide for Personal Computers. Release 6.03 Edition. Cary, North Carolina.

Sullivan, L. F., D. A. Emiliani, and K. N. Baxter. 1985. Standing stock of juvenile brown shrimp, *Penaeus aztecus*, in Texas coastal ponds. Fishery Bulletin 83:677-682.

Turner, R. E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106:411-416.

U. S. Department of Commerce. 1990. Fisheries of the United States, 1989. Current Fisheries Statistics Number 8900.

Walker, H. J., J. M. Coleman, H. H. Roberts, and R. S. Tye. 1987. Wetland loss in Louisiana. Geografiska annaler 69A:189-200.

Wicker, A. M., B. M. Currin, and J. M. Miller. 1988. Migration of brown shrimp in nursery areas of Pamlico Sound, North Carolina, as indicated by changes in length-frequency distributions. Transactions of the American Fisheries Society 117:92-94.

Zein-Eldin, Z. P. 1963. Effects of salinity on growth of postlarval penaeid shrimp. Biological Bulletin (Woods Hole) 125:188-196.

Zein-Eldin, Z. P., and M. L. Renaud. 1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus* populations in coastal waters, particularly of Texas. Marine Fisheries Review 48(3):9-19.

Zimmerman, R. J., and T. J. Minello. 1984. Densities of *Penaeus aztecus, P. setiferus* and other natant macrofauna in a Texas salt marsh. Estuaries 7: 421-433.

VITA

E. Eric Knudsen was born in Willamantic, CT in 1948. He graduated from West Springfield High School, West Springfield, MA in 1966. He served in the U.S. Coast Guard from 1966 to 1970.

In 1970, Eric began his career in fisheries biology by enrolling in the University of Massachusetts at Amherst and graduated, cum laude, in 1974. During the summers of 1972 and 1973 he worked for the Massachusetts Cooperative Fishery Unit and the Vermont Fish and Game Department.

Eric earned his M.S. in fisheries at Louisiana State University in 1976. He studied brown shrimp ecology at Rockefeller Wildlife Refuge.

He worked for the U.S. Fish and Wildlife Service in Olympia Washington from 1976 to 1980. In 1981, Eric returned to Louisiana State University as a Research Associate and directed the day-to-day activities of the Cameron-Creole Study. Eric became a Ph.D. candidate in 1985.

In 1987, Eric returned to the Fish and Wildlife Service and is presently a Supervisory Fishery Biologist, involved primarily in the restoration of depleted Pacific salmon runs.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Everett Eric Knudsen

Major Field: Wildlife and Fisheries Science

Title of Dissertation: JUVENILE PENAEID SHRIMP ECOLOGY IN A LOUISIANA COASTAL MARSH MANAGEMENT AREA

Approved:

William H. Herke
Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

William E. Kelso

Mark K. Johnson

Ronald L. Thune

Richard Condrey

Robert B Hamilton

C.F. Bryan

Date of Examination:

November 30, 1990